

# Effects of soil temperature on parameters of a coupled photosynthesis–stomatal conductance model

TIEBO CAI<sup>1</sup> and QING-LAI DANG<sup>1,2</sup>

<sup>1</sup> Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada

<sup>2</sup> Author to whom correspondence should be addressed (dangqinglai@aol.com)

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**Summary** To examine the effects of soil temperature on a coupled photosynthesis–stomatal conductance model, seedlings of trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea Mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss) were exposed to soil temperatures ranging from 5 to 35 °C for 4 months. Light and CO<sub>2</sub> response curves of foliar gas exchange were measured for model parameterization. The effects of soil temperature on four key model parameters,  $V_{\text{cmax}}$  (maximum rate of carboxylation),  $J_{\text{max}}$  (maximum rate of electron transport),  $\alpha$  (energy conversion efficiency or quantum efficiency of electron transport) and  $R_d$  (daytime dark respiration), were modeled using two third-order polynomial equations and a modified Arrhenius equation. In all species,  $V_{\text{cmax}}$  and  $J_{\text{max}}$  increased with soil temperature up to an optimum, and then decreased with further increases in soil temperature. In the conifers,  $\alpha$  showed a similar response to soil temperature as  $V_{\text{cmax}}$  and  $J_{\text{max}}$ , but soil temperature had no significant effect on  $\alpha$  in aspen. Soil temperature had no significant effect on  $R_d$  in any species. The three equations described the relationships between soil temperature and the model parameters reasonably well, but performed best for  $V_{\text{cmax}}$  and worst for  $\alpha$ . No significant relationships were identified between soil temperature and the parameters of the stomatal conductance model.

**Keywords:** black spruce, boreal forest, gas exchange, jack pine, photosynthesis model, trembling aspen, white spruce.

## Introduction

A coupled photosynthesis–stomatal conductance model ( $A-g_s$  model) is often employed to simulate and predict ecophysiological responses of forest ecosystems and their acclimation to changing environmental conditions (Farquhar et al. 1980, Leuning 1990, Collatz et al. 1991, Harley et al. 1992, Nikolov et al. 1995, Niinemets and Tenhunen 1997) and to scale the response in space and time (Baldocchi and Harley 1995, Leuning 1995, Lloyd et al. 1995, Sellers et al. 1996, de Pury and Farquhar 1997, Wang and Leuning 1998). However, the parameters of such a model are generally derived from data collected under constant soil conditions (Dang et al. 1998). Although models are available for predicting soil temperatures

from climate variables, such as air temperature and precipitation (Bonan 1991, Yin and Arp 1993), it is difficult to incorporate such models into ecophysiological models, such as the  $A-g_s$  model, because of the lack of information on how soil temperatures affect model parameters. As a result, the accuracy of ecophysiological models is limited, particularly when applied to areas with distinctly different soil temperatures or when incorporated into larger-scale models (Sellers et al. 1996).

Leuning (1995) pointed out that the parameters of the  $A-g_s$  model, when scaled up to the regional or global level, are not universally constant, but vary in space and time and are unknown for most ecosystems. Because of the nonlinear relationships between plant physiological processes and environmental variables, extrapolation of results from a few sites to large regions is difficult (Luxmoore et al. 1991, Kimball et al. 2000). For example, boreal broadleaf forests have lower photosynthetic capacities than their equivalents in temperate regions (Baldocchi and Harley 1995), and even in the same boreal ecosystem, northern species have lower photosynthetic capacities than their southern counterparts (Dang et al. 1998). This difference in photosynthetic capacity is partly attributed to the difference in soil temperature (Baldocchi and Harley 1995, Dang et al. 1998). Net  $A$  is more sensitive to changes in soil temperature than to changes in air temperature (Schwarz et al. 1997). Consideration of soil heterogeneity in temperature (Luxmoore et al. 1991), physical and other properties (Running et al. 1989), is critical for understanding land–atmosphere interactions in global circulation models (Sellers et al. 1997). The boreal forest represents a complex land cover mosaic (Kimball et al. 2000) with great variation in soil temperature, which ranges from near zero over permafrost to 35 °C on south-facing slopes and newly burned sites (Bonan and Shugart 1989). Hence it is necessary to take soil temperature into consideration when scaling up the  $A-g_s$  model to the entire boreal forest ecosystem.

The objective of this study was to investigate and model the effects of soil temperature on the parameters of a coupled  $A-g_s$  model. This study forms part of a larger project investigating the ecophysiological response of boreal trees to soil temperature.

## Materials and methods

### Plant materials

One-year-old seedlings of black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.) were obtained from A&R Container Tree Seedling Nursery in Dorion, Ontario. Aspen seedlings (*Populus tremuloides* Michx.) were grown from seeds in the Lakehead University greenhouses and cold-hardened at the end of the fourth month by exposing them to day/night temperatures of 15/5 °C and an 8-h photoperiod. All seedlings were stored at 2 °C before initiation of the experiment.

### Experimental design

The experiment was carried out in two greenhouses. Each greenhouse contained seven soil temperature treatments: 5, 10, 15, 20, 25, 30 and 35 °C. Each soil temperature treatment was conducted in a separate box. Each box contained eight rows of 14 containers (13.5-cm tall, 11 cm top diameter) mounted to the bottom. A drain-hole (1.3-cm diameter) was drilled through the bottom of the box under each container. Soil temperature was controlled by circulating temperature-controlled water among the containers inside the box. The boxes were insulated so that the soil temperature was independent of the air temperature in the greenhouse. Both soil temperatures and greenhouse air temperature were monitored continuously with an SCXI-MS100 temperature system (National Instruments, Austin, TX) connected to a computer. Mean daily soil temperature was generally within  $\pm 0.41$  °C of the set value (see Cheng et al. 2000 for more details on soil temperature control). The seven boxes were randomly located in each greenhouse. Each species was randomly assigned to two rows of containers within each soil temperature box.

### Growing conditions

Mean day and night air temperatures in the greenhouse were 22.5 and 14.3 °C, respectively. The experiment started on February 6, 1999. High-pressure sodium lamps were used to extend the natural photoperiod to 16 h in the early part of the experiment. The growing medium was a 1:1 (v/v) mixture of peat moss and vermiculite. Seedlings were watered to saturation every second day with a nutrient solution containing 126 ppm N, 44 ppm P, 83 ppm K, 40 ppm Mg, 52 ppm S, 30 ppm Ca, 2.5 ppm Fe, 0.67 ppm Mn, 0.4 ppm Zn, 0.3 ppm Cu, 0.12 ppm B and 0.003 ppm Mo (Landis et al. 1989). The electrical conductivity of the growing medium (1.3 mS cm<sup>-1</sup>) was less than the threshold value (2.2 mS cm<sup>-1</sup>) recommended by Landis et al. (1989). Soil pH was about 5.9 during the experiment.

### Gas exchange measurement

The response curves of  $A$  and  $g_s$  to photosynthetically active radiation (PAR; 22 °C, 350 ppm CO<sub>2</sub>, 50% RH) and CO<sub>2</sub> partial pressure (1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR, 22 °C, 50% RH) were measured with a CIRGA-1 gas exchange system and Parkinson leaf chambers (PP-Systems, Haverhill, MA). The PAR, CO<sub>2</sub> concentration, humidity and leaf temperature inside both

the conifer chamber and the broadleaf chamber were controlled automatically by the system. A conifer twig (< 9-cm long) or a leaf section of aspen (2.5-cm<sup>2</sup> disk) was enclosed in the leaf chamber for measurement. The seedling remained in the soil temperature control box during the measurement. One seedling from each row of each soil temperature box was randomly selected for measurement. Four seedlings were measured for each soil temperature  $\times$  species combination.

## Model description

### Photosynthesis sub-model

We used the modified version (Harley et al. 1992) of the biochemical model for CO<sub>2</sub> assimilation ( $A$ ) developed by Farquhar et al. (1980):

$$A = \left(1 - \frac{0.5O}{\tau C_i}\right) \min\{W_c, W_j\} - R_d, \quad (1)$$

where  $C_i$  and  $O$  are CO<sub>2</sub> and O<sub>2</sub> partial pressures in the intercellular space, respectively,  $R_d$  is daytime dark respiration,  $\tau$  is the specificity factor for Rubisco (Jordan and Ogren 1984),  $W_c$  is carboxylation rate determined by the amount, activity, and kinetic properties of Rubisco,  $W_j$  is rate of carboxylation determined by the rate of RuBP regeneration and  $\min\{W_c, W_j\}$  denotes the minimum of the two. We did not consider sink limitation (Sharkey 1985, Harley and Sharkey 1991) or co-limitations (Collatz et al. 1991). Parameter  $W_c$  was calculated as:

$$W_c = \frac{V_{\text{cmax}} C_i}{C_i + K_c \left(1 + \frac{O}{K_o}\right)}, \quad (2)$$

where  $V_{\text{cmax}}$  is maximum rate of carboxylation and  $K_c$  and  $K_o$  are the Michaelis constants for carboxylation and oxygenation, respectively. Parameter  $W_j$  was calculated as:

$$W_j = \frac{J C_i}{4 \left(C_i + \frac{O}{\tau}\right)}, \quad (3)$$

where  $J$  is potential rate of electron transport (Farquhar and von Caemmerer 1982, Harley et al. 1992) and was calculated according to Smith (1937) and Harley et al. (1992):

$$J = \frac{\alpha Q_p}{\sqrt{1 + \frac{\alpha^2 Q_p^2}{J_{\text{max}}^2}}}, \quad (4)$$

where  $\alpha$  is the energy conversion efficiency of incident light (mol electron mol<sup>-1</sup> photon),  $Q_p$  is photosynthetically active radiation flux density and  $J_{\text{max}}$  is light-saturated rate of electron transport.

The temperature dependencies of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  are described in Johnson et al. (1942), Tenhunen et al. (1976), and Harley and Tenhunen (1991):

$$P = \frac{P(T_{\text{ref}}) e^{\left( \frac{\Delta H_a}{RT_{\text{ref}}} \left( 1 - \frac{T_{\text{ref}}}{T_k} \right) \right)}}{1 + e^{\left( \frac{\Delta S T_k - \Delta H_d}{RT_k} \right)}}, \quad (5)$$

where  $P$  is either  $V_{\text{cmax}}$  or  $J_{\text{max}}$  and  $P(T_{\text{ref}})$  is the value of either  $V_{\text{cmax}}$  or  $J_{\text{max}}$  at the reference temperature  $T_{\text{ref}}$  (normally 25 °C) in the absence of high temperature deactivation (Wohlfahrt et al. 1998),  $\Delta H_a$  is activation energy,  $\Delta H_d$  is deactivation energy,  $\Delta S$  is an entropy term,  $T_k$  is absolute leaf temperature and  $R$  is the gas constant (8.314 J K<sup>-1</sup> mol<sup>-1</sup>).

The temperature dependencies of  $\tau$ ,  $K_c$ ,  $K_o$  and  $R_d$  are described by an Arrhenius equation:

$$P = P(T_{\text{ref}}) e^{\left( \frac{\Delta H_a}{RT_{\text{ref}}} \left( 1 - \frac{T_{\text{ref}}}{T_k} \right) \right)}, \quad (6)$$

where  $P$  is any of the above parameters.

Equation 1 is driven by  $C_i$ , and  $C_i$  and  $A$  are linked by Equation 7:

$$C_i = C_s - \frac{A1.6(100)}{g_s}, \quad (7)$$

where  $C_s$  is CO<sub>2</sub> partial pressure at the leaf surface and  $g_s$  is stomatal conductance to H<sub>2</sub>O.

#### Stomatal conductance sub-model

To model gas-exchange responses to changing environmental conditions, the photosynthesis model must be coupled with a  $g_s$  model. We used the empirical  $g_s$  model developed by Ball et al. (1987):

$$g_s = b + m(100)A \frac{h_s}{C_s}, \quad (8)$$

where  $h_s$  is relative humidity (decimal) and  $b$  and  $m$  are regression coefficients. We did not consider the effect of patchy stomatal closure (Mott 1995, Buckley et al. 1997, Haefner et al. 1997).

#### Model parameterization

The values  $K_c = 32.9$  Pa,  $K_o = 39.7$  kPa and  $\tau = 2337.28$  at 25 °C were adopted from Jordan and Ogren (1984). The original units of  $K_c$  and  $K_o$  were  $\mu\text{M}$ , which we converted to Pa based on the solubility of CO<sub>2</sub> and O<sub>2</sub> (0.334  $\mu\text{M} = 1$  Pa and 0.0126  $\mu\text{M} = 1$  Pa, respectively) according to von Caemmerer et al. (1994). We calculated  $\Delta H_a$  from the slope ( $b$ ) of linear regressions of  $\ln(K_c)$  or  $\ln(K_o)$  or  $\ln(\tau)$  versus  $1/T$  (where  $T$  is temperature in K), ( $\Delta H_a = -8.314b$ , Chang 1994). All values are given in Table 1.

We used the average  $\Delta H_a$ ,  $\Delta S$  and  $\Delta H_d$  values from the litera-

ture for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (Farquhar et al. 1980, Harley and Tenhunen 1991, Harley et al. 1992, Falge et al. 1996, Walcroft et al. 1997, Wohlfahrt et al. 1998) (Table 1). The apparent quantum yield ( $\phi$ ) of photosynthesis was estimated from the slope of the initial, linear part (PAR < 150  $\mu\text{mol}^{-1} \text{m}^{-2} \text{s}^{-1}$ ) of photosynthetic light response curves. We calculated  $\alpha$  as  $\alpha = 4\phi$ . We used the intercept of the linear regression as an estimate of dark respiration ( $R_{\text{dark}}$ ) and used half of this value as the estimate of  $R_d$  (Wohlfahrt et al. 1998). By substituting Equation 3 into Equation 2, together with estimated values of  $\tau$ ,  $K_c$ ,  $K_o$ ,  $O$  (20.9 kPa) and  $R_d$ ,  $V_{\text{cmax}}$  was estimated from the initial part of the  $A/C_i$  curve with Equation 9:

$$A = \frac{V_{\text{cmax}} C_i}{C_i + K_c \left( 1 + \frac{O}{K_o} \right)} \left( 1 - \frac{0.5O}{\tau C_i} \right) - R_d. \quad (9)$$

With  $V_{\text{cmax}}$ ,  $\alpha$  and  $R_d$  determined,  $J_{\text{max}}$  was estimated by fitting Equation 1 to the entire CO<sub>2</sub> response curve using the non-linear least squares technique.

The  $g_s$  model was parameterized with the pooled data from the temperature response, CO<sub>2</sub> response and PAR response measurements. To estimate parameters  $b$  and  $m$ ,  $g_s$  was regressed against the combined variable  $Ah_s100/C_s$ . As suggested by Ball et al. (1987) and Harley et al. (1992), data with  $C_s < 30$  Pa or PAR < 150  $\mu\text{mol}^{-1} \text{m}^{-2} \text{s}^{-1}$  were not used.

#### Data analysis

Equations 10–12 were used to model the relationships of  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  and  $\alpha$  with soil temperature:

$$P = a_1 + b_1 T_s + c_1 T_s^2 + d_1 T_s^3, \quad (10)$$

$$P = P(T_{s25}) \left( 1 + a_2 (T_s - 25) + b_2 (T_s - 25)^2 + c_2 (T_s - 25)^3 \right), \quad (11)$$

$$P = \frac{P(T_{s25}) e^{\left( \frac{\Delta H_a}{R298} \left( 1 - \frac{298}{T_s} \right) \right)}}{1 + e^{\left( \frac{\Delta S T_s - \Delta H_d}{RT_s} \right)}}, \quad (12)$$

where  $P$  represents  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  or  $\alpha$ ,  $P(T_{s25})$  is the mean value of  $P$  at 25 °C soil temperature,  $a_1$ ,  $b_1$ ,  $c_1$ ,  $d_1$ ,  $a_2$ ,  $b_2$  and  $c_2$  are regression coefficients,  $\Delta H_a$ ,  $\Delta H_d$ ,  $\Delta S$  and  $R$  are as in Equation 5,  $T_s$  is soil temperature in °C in Equations 10 and 11 and in K in Equation 12. Equation 11 was adapted from Kirschbaum and Farquhar (1984), and Equation 12 from Harley et al. (1992).

The coefficients in the above equations were estimated using the Marquardt-Levenberg nonlinear regression algorithm in the curve-fitting program of SigmaPlot 2000 (SPSS, Chicago, IL). Because the residuals for  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  and  $\alpha$  were homogeneous across all soil temperatures and species, no weighting to the residuals was used in the curve-fitting procedure.

Table 1. List of model parameters and their temperature dependencies. The values for daytime dark respiration ( $R_d$ ), maximum rate of carboxylation ( $V_{cmax}$ ) and light-saturated rate of electron transport ( $J_{max}$ ) were the averages of values for different  $C_3$  plants in the literature. The values of the Michaelis constants for carboxylation and oxygenation ( $K_c$  and  $K_o$ , respectively) were taken from Jordan and Ogren (1984, for spinach). The reference temperature was 298 K. Abbreviations:  $\tau$  = specificity factor for Rubisco;  $\Delta H_a$  = activation energy;  $\Delta H_d$  = deactivation energy; and  $\Delta S$  = entropy term.

Parameter	Units	Temperature parameters	Values	Units
$K_c$	Pa CO <sub>2</sub>	$\Delta H_a$	59789	J mol <sup>-1</sup>
$K_o$	kPa O <sub>2</sub>	$\Delta H_a$	1397	J mol <sup>-1</sup>
$\tau$		$\Delta H_a$	-20970	J mol <sup>-1</sup>
$R_d$	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$\Delta H_a$	48294	J mol <sup>-1</sup>
$V_{cmax}$	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$\Delta H_a$	75794	J mol <sup>-1</sup>
		$\Delta H_d$	202022	J mol <sup>-1</sup>
		$\Delta S$	657	J K <sup>-1</sup> mol <sup>-1</sup>
$J_{max}$	$\mu\text{mol electrons m}^{-2} \text{ s}^{-1}$	$\Delta H_a$	58936	J mol <sup>-1</sup>
		$\Delta H_d$	199233	J mol <sup>-1</sup>
		$\Delta S$	647	J K <sup>-1</sup> mol <sup>-1</sup>

Analysis of variance (ANOVA) was conducted to test soil temperature effects on  $V_{cmax}$ ,  $J_{max}$  and  $\alpha$  using DataDesk 6.0 statistical software (1996; Data Description, Ithaca, NY). Tests showed that the data met all the assumptions for ANOVA. When  $P > 0.25$ , insignificant interactions were pooled. When interactions were significant ( $P < 0.05$ ), the examination of treatment effects proceeded from the interaction with the highest order, to lower order interactions and then to main effects (Brown 1995). Because variation in  $g_s$  model parameters was irregular, the data for all species and soil temperatures were pooled to produce a single equation and no further tests were performed.

## Results

### Effects of soil temperature on maximum rate of carboxylation

In all species,  $V_{cmax}$  increased with increasing soil temperature from 5 °C to an optimum (generally around 25 °C), then decreased with further increases in soil temperature (Figures 1a–d). When Equation 10 was used to model the relationship, there were large variations in all coefficients between species but with no specific pattern (Table 2). The between-species variation in coefficients was much smaller for Equations 11 and 12 than for Equation 10 (Tables 3 and 4). Equations 10–12 fit the measured  $V_{cmax}$  well in all species (Figure 1, Tables 2–4).

Aspen had significantly higher  $V_{cmax}$  than the conifers ( $P < 0.05$ , Figure 1e). Among the conifers, white spruce had significantly smaller  $V_{cmax}$  than jack pine and black spruce ( $P < 0.05$ ), but the difference between black spruce and jack was not significant ( $P = 0.62$ ).

### Effects of soil temperature on light-saturated rate of electron transport

In all species,  $J_{max}$  varied with soil temperature in the same manner as  $V_{cmax}$ , though  $J_{max}$  showed greater variability (Fig-

ures 1 and 2). Equations 10–12 fit the data reasonably well but  $R^2$  was generally smaller for  $J_{max}$  than for  $V_{cmax}$  (Tables 2–4).

Values of  $J_{max}$  were significantly greater for aspen than for

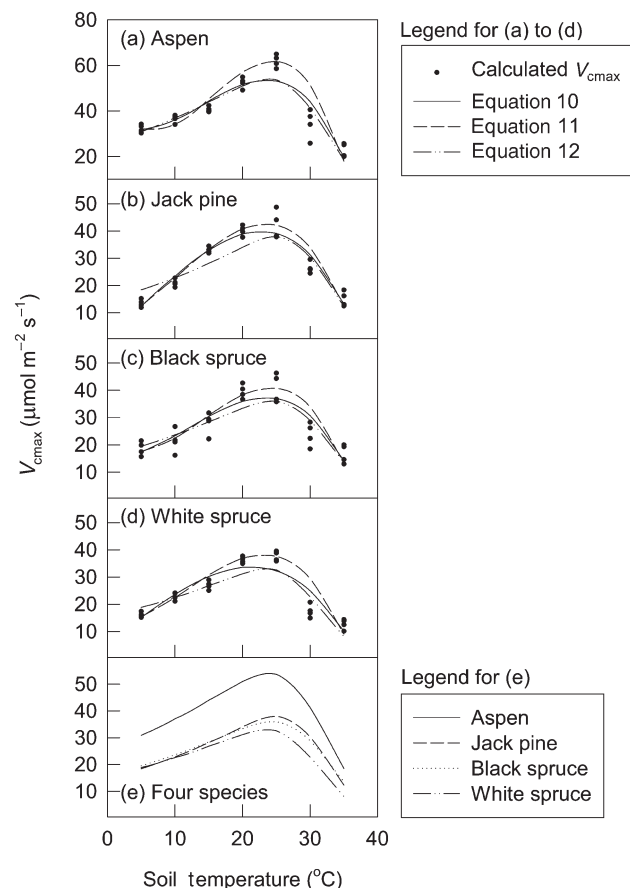


Figure 1. Relationship between maximum rate of carboxylation ( $V_{cmax}$ ) and soil temperature for aspen, jack pine, black spruce and white spruce. Figure 1e was generated with Equation 12 (see Tables 2–4 for parameter values).

Table 2. Coefficients of Equation 10 ( $a_1$ ,  $b_1$ ,  $c_1$  and  $d_1$ ) for maximum rate of carboxylation ( $V_{\text{cmax}}$ ), light-saturated rate of electron transport ( $J_{\text{max}}$ ) and energy conversion efficiency of incident light ( $\alpha$ ). For all parameters and all species  $P < 0.05$ . Soil temperature had no significant effect on  $\alpha$  in aspen.

Parameter	Species	$a_1$	$b_1$	$c_1$	$d_1$	$R^2$
$V_{\text{cmax}}$	Aspen	35.83	-1.99	0.27	-0.006	0.77
	Jack pine	2.25	1.78	0.06	-0.0029	0.90
	Black spruce	15.61	-0.24	0.14	-0.0038	0.73
	White spruce	6.34	1.72	0.02	-0.0019	0.79
$J_{\text{max}}$	Aspen	85.53	-3.91	0.59	-0.015	0.79
	Jack pine	19.44	4.68	0.047	-0.0047	0.71
	Black spruce	62.27	-3.58	0.57	-0.0136	0.57
	White spruce	18.04	4.79	0.046	-0.00464	0.72
$\alpha$	Jack pine	0.064	0.011	-0.0000052	-0.00000055	0.56
	Black spruce	0.078	0.012	-0.00015	-0.0000004	0.77
	White spruce	0.086	0.017	-0.00067	-0.00000078	0.52

the conifers ( $P < 0.05$ , Figure 2e). Values of  $J_{\text{max}}$  were also significantly greater for black spruce than for jack pine and white spruce ( $P < 0.05$ ), but there was no significant difference between white spruce and jack pine ( $P = 0.84$ , Figure 2e). For all species,  $J_{\text{max}}$  was closely correlated to  $V_{\text{cmax}}$  (Figure 3).

#### Effects of soil temperature on the energy conversion efficiency of photosynthesis

Soil temperature significantly affected  $\alpha$  in the three conifers ( $P < 0.05$ ) but not in aspen ( $P = 0.10$ ) (Figure 4). The  $\alpha$  response patterns for conifers were similar to those of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (Figures 1, 2 and 4), but the relationship was not as tight as that for  $V_{\text{cmax}}$  and  $J_{\text{max}}$ . Equations 10 and 12 performed poorly in describing the relationship between  $\alpha$  and soil temperature (Tables 2–4).

Aspen had significantly higher  $\alpha$  than the conifers ( $P < 0.05$ ). Among the conifers,  $\alpha$  was higher for jack pine than for the spruces and there was no significant difference between the two spruce species ( $P = 0.21$ , Figure 4e).

#### Effects of soil temperature on daytime dark respiration

There were no significant differences in  $R_d$  among soil temperatures ( $P = 0.42$ ) or tree species ( $P = 0.32$ ). Values of  $R_d$  ranged from 0.01 to 1.5, but most of the data varied between 0.3 and 0.9 with a grand mean of  $0.53 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

#### Effects of soil temperature on the stomatal conductance model

Variation in parameters for the  $g_s$  model did not show any regularity between species or between soil temperatures within a species (data not shown). Therefore, a single parameterization was done for all the species and all soil temperatures together (Figure 5).

#### Discussion

We obtained evidence that, to ensure the accuracy of model estimation of gas exchange between trees and the atmosphere, soil temperature should be considered in the photosynthesis

Table 3. Coefficients of Equation 11 ( $a_2$ ,  $b_2$  and  $c_2$ ) for maximum rate of carboxylation ( $V_{\text{cmax}}$ ), light-saturated rate of electron transport ( $J_{\text{max}}$ ) and energy conversion efficiency of incident light ( $\alpha$ ). For all parameters and all species  $P < 0.05$ . Soil temperature had no significant effect on  $\alpha$  in aspen.

Parameter	Species	$a_2$	$b_2$	$c_2$	$R^2$
$V_{\text{cmax}}$	Aspen	-0.0050	-0.0048	-0.00017	0.62
	Jack pine	-0.0139	-0.0046	-0.00011	0.87
	Black spruce	-0.0074	-0.0046	-0.00014	0.68
	White spruce	-0.0169	-0.0047	-0.00011	0.69
$J_{\text{max}}$	Aspen	-0.005	-0.004	-0.00013	0.74
	Jack pine	-0.018	-0.003	-0.0000489	0.71
	Black spruce	-0.003	-0.0046	-0.000158	0.52
	White spruce	-0.011	-0.0040	-0.0000987	0.65
$\alpha$	Jack pine	-0.0059	-0.0033	-0.0000087	0.41
	Black spruce	-0.0094	-0.0022	-0.0000032	0.76
	White spruce	-0.0075	-0.00044	-0.0000033	0.52



Table 4. Coefficients of Equation 12 for maximum rate of carboxylation ( $V_{\text{cmax}}$ ), light-saturated rate of electron transport ( $J_{\text{max}}$ ) and energy conversion efficiency of incident light ( $\alpha$ ). Abbreviations:  $\Delta H_a$  = activation energy;  $\Delta S$  = entropy term; and  $\Delta H_d$  = deactivation energy. For all parameters and all species  $P < 0.05$ . Soil temperature had no significant effect on  $\alpha$  in aspen.

Parameter	Species	$\Delta H_a$	$\Delta S$	$\Delta H_d$	$R^2$
$V_{\text{cmax}}$	Aspen	23883	792	240871	0.82
	Jack pine	28526	899	273437	0.80
	Black spruce	25410	796	242404	0.71
	White spruce	23690	889	269756	0.79
$J_{\text{max}}$	Aspen	20168	821	250926	0.80
	Jack pine	16861	840	257233	0.57
	Black spruce	26401	765	232804	0.57
	White spruce	23719	736	224307	0.68
$\alpha$	Jack pine	20531	563	172688	0.54
	Black spruce	14008	641	198005	0.63
	White spruce	6946	555	175010	0.30

sub-model of the coupled  $A-g_s$  model but not in the  $g_s$  sub-model. Soil temperature had significant effects on three key parameters of the photosynthesis model:  $V_{\text{cmax}}$  and  $J_{\text{max}}$  in all

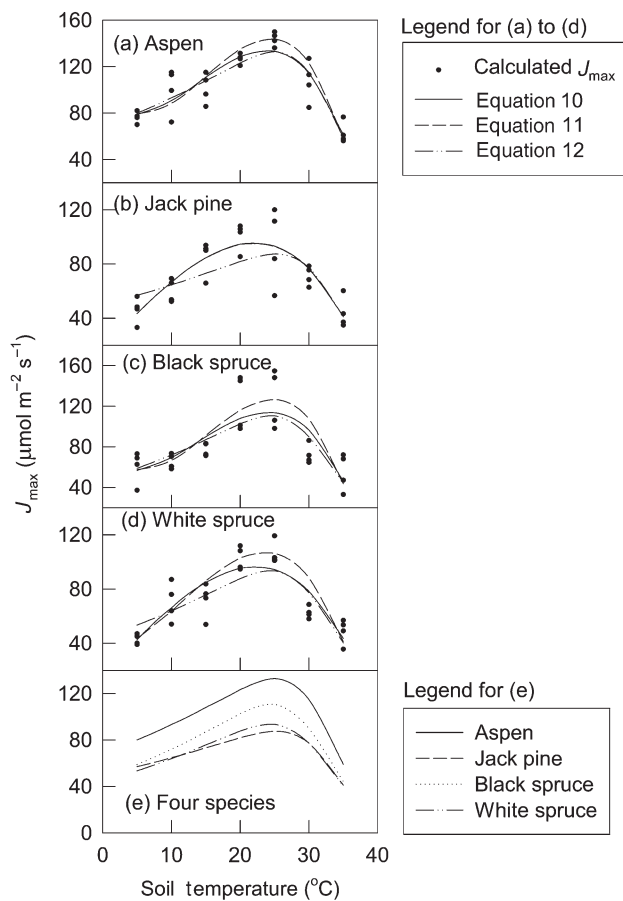


Figure 2. Relationship between light-saturated rate of electron transport ( $J_{\text{max}}$ ) and soil temperature for aspen, jack pine, black spruce and white spruce. Figure 2e was generated with Equation 12 (see Tables 2–4 for parameter values). The lines for Equations 10 and 11 overlapped for jack pine.

four species and  $\alpha$  in the three conifers. The parameters decreased as soil temperature deviated from the optimum. Such effects can be simulated with the model developed in this study. Soil temperature did not significantly affect the parameters of the  $g_s$  sub-model.

The four boreal tree species optimized resource allocation among the component systems of photosynthesis. Parameter  $V_{\text{cmax}}$  reflects nitrogen investment in Rubisco and  $J_{\text{max}}$  reflects nitrogen investment in Photosystem II complex and cytochrome  $f$  in the photosystem (Hikosaka 1997). Despite large differences in photosynthetic capacity among trees exposed to different soil temperatures,  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were highly correlated (Figure 3), suggesting that these boreal tree species optimized their resource allocation (particularly nitrogen) between the biochemical and photochemical machinery of photosynthesis in response to large differences in soil temperature (5 to 35 °C). Similar phenomena have been reported for other species and environmental conditions (Thompson et al. 1992, Wullschleger 1993). Thompson et al. (1992) found an internal consistency between  $V_{\text{cmax}}$  and  $J_{\text{max}}$  for four species in two nutrient and three light regimes. Kingston-Smith et al. (1999) found a virtually identical relationship between Photo-

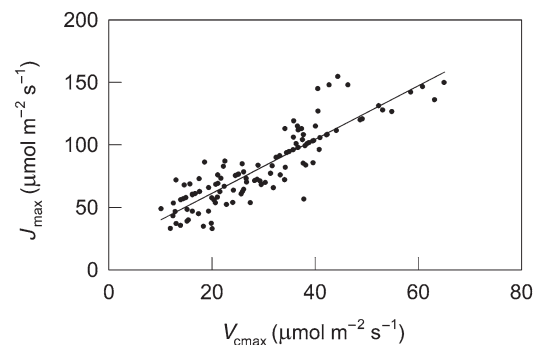


Figure 3. Relationship between maximum rate of carboxylation ( $V_{\text{cmax}}$ ) and light-saturated rate of electron transport ( $J_{\text{max}}$ ) for all species. Regression:  $J_{\text{max}} = 2.15V_{\text{cmax}} + 18.39$  ( $r^2 = 0.78$ ).

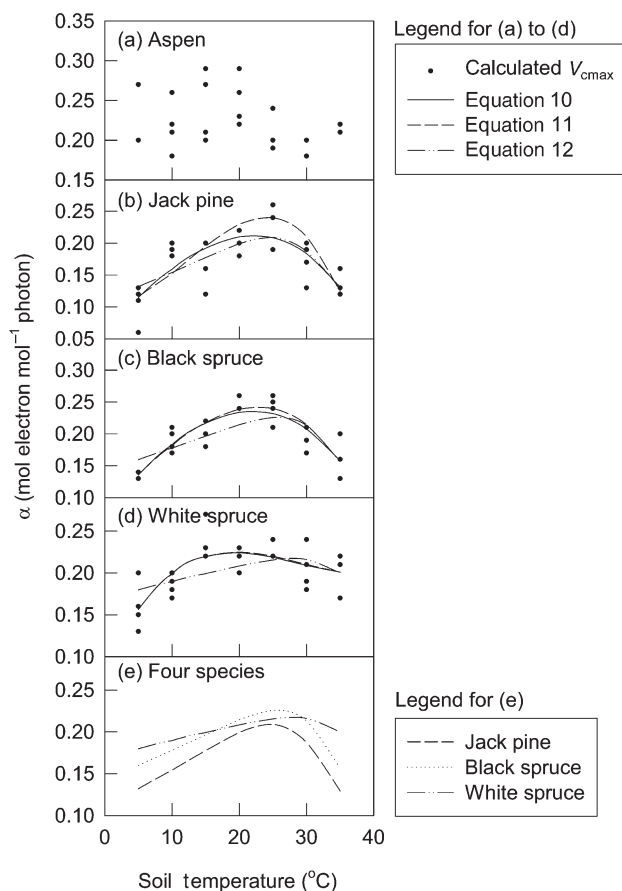


Figure 4. Relationship between energy conversion efficiency of incident light ( $\alpha$ ) and soil temperature for aspen, jack pine, black spruce and white spruce. Figure 4e was generated with Equation 12 (see Tables 2–4 for parameter values). There was no significant correlation between  $\alpha$  and soil temperature for aspen.

system I and Photosystem II in maize (*Zea mays* L.) plants grown at air temperatures of 14 and 20 °C and concluded that maize plants preserved the integrity of photosynthetic electron

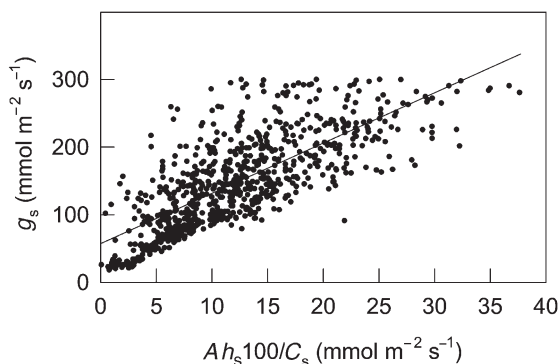


Figure 5. Relationship between stomatal conductance ( $g_s$ ) and the combined variable of  $Ah_s100/C_s$ , where  $A$  =  $\text{CO}_2$  assimilation and  $h_s$  and  $C_s$  are relative humidity and  $\text{CO}_2$  partial pressure at the leaf surface, respectively, for all four species. Model:  $g_s = 57.34 + 7.43Ah_s100/C_s$  ( $r^2 = 0.56$ ).

transport system and its co-ordination with  $\text{CO}_2$  assimilation at low growth temperatures. Flexas et al. (1999) reported that a close link between electron transport rate and  $\text{CO}_2$  assimilation was maintained in young potted grapevines (*Vitis vinifera* L. cv. Tempranillo) in different water supply regimes.

We found that the four boreal species optimized their photosynthetic carbon gain with respect to transpirational water loss at different soil temperatures. Our simulation results (not shown) suggest that, in all species, photosynthesis operated at internal  $\text{CO}_2$  concentrations ( $C_i$ ) such that it was co-limited by  $W_c$  and  $J_c$ . A higher  $C_i$  would have increased the efficiency of photosynthetic nitrogen use but decreased water-use efficiency and vice versa. Operating at the co-limiting point represents a compromise between water-use efficiency and nitrogen-use efficiency (Lambers et al. 1998, Franks and Farquhar 1999), optimizing photosynthetic carbon gain relative to the cost of transpirational water loss (Wong et al. 1979). These results also suggest that the species decreased their photosynthetic capacity at unfavorable soil temperatures where water uptake by roots was limited. This is consistent with the finding of Terashima (1992) that the decrease in photosynthesis in chronically water-stressed plants is caused by down-regulation of photosynthesis.

The three conifers suffered more severe stress at unfavorable soil temperatures than aspen. The energy conversion efficiency of photosynthesis ( $\alpha$ ) (or quantum efficiency of electron transport) is sensitive to environmental stresses, such as photoinhibition (Powles 1984), heat (Berry and Björkman 1980) and low leaf water potential (Mohanty and Boyer 1976), but it is almost constant in non-stressed  $\text{C}_3$  plants (Ehleringer and Björkman 1977, Sharkey 1985, Harley et al. 1992, Long et al. 1993). Variation in soil temperature had significant effects on  $\alpha$  in the three conifers but not in aspen, suggesting the conifers suffered more stresses than aspen. This result is consistent with the finding of Dang et al. (1997) that photosynthesis of aspen is not significantly affected by the low water potentials that substantially reduce the photosynthesis of jack pine and black spruce.

We found that variation in  $R_d$  ( $0\text{--}1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) had no significant effects on the estimation of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (data not shown). This result is consistent with published reports that the correlation coefficient between  $V_{\text{cmax}}$  and  $R_d$  ranges from 0.0052 to 0.038 (Collatz et al. 1991, Sellers et al. 1996, Niinemets and Tenhunen 1997, Wohlfahrt et al. 1998).

Our findings indicate that model parameters derived from young trees can be applied to large trees in the field, provided that precautions are exercised. The parameters for the photosynthesis sub-model at optimal soil temperatures (such as  $V_{\text{cmax}}$ ) were generally greater than those for mature trees of the same species grown in the field (Dang et al. 1998). However, we note that the field measurements were made under sub-optimal soil temperature and other environmental conditions. Additionally Dang et al. (1998) used semi-surface leaf area, whereas we used projected leaf area for the calculation of gas exchange parameters. Dang et al. (1998) also used larger twigs, resulting in a greater extent of self-shading between fo-

liage and thus a lower photosynthetic rate. After considering the differences in these two studies, we conclude that the parameters derived in our study correspond well with the values for large field-grown trees of the same species. Nevertheless, large trees may respond differently to changes in soil temperature than seedlings. Also, field environmental conditions are more variable than greenhouse conditions, for example, soil temperatures vary both spatially (with depth and sites) and temporally (diurnally and seasonally). Therefore, calibrations and further studies are needed before the results can be applied to field conditions, particularly where high resolution is required.

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