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Simulating carbon exchange in Canadian Boreal forests I. Model structure, validation, and sensitivity analysis

Xiaolu Zhou[a], *Changhui Peng*[a,*], *Qing-Lai Dang*[b], *Jianfeng Sun*[a], *Haibin Wu*[a], *Dong Hua*[a,b]

[a] *Institut des sciences de l'environnement, Département des sciences biologiques, Université du Quebec à Montréal, Case postale 8888, Succursale Centre-Ville, Montréal, QC H3C 3P8, Canada*

[b] *Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada*

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ABSTRACT

This paper will discuss TRIPLEX-Flux, a process-based model that estimates net ecosystem production (NEP) as well as analyzing the level of sensitivity of the model's response by simulating CO_2 flux in an existing old black spruce BOREAS site in central Canada. The research objectives were: (1) to test the TRIPLEX-Flux model simulations against flux tower measurements; and (2) to examine parameter and input variable effects on model response via sensitivity analysis. Validation of NEP data at 30 min intervals derived from tower and chamber measurements showed that the NEP data from the model corresponded well with the measured NEP from the BOREAS site ($R^2 > 0.65$). Sensitivity analysis demonstrated different levels of sensitivity between morning and noon periods and from the current to doubled atmospheric CO_2 concentrations. Additionally, the comparison of different algorithms to calculate stomatal conductance showed that the NEP predicted by the model using the iteration algorithm was consistent with the results using a constant C_i/C_a of 0.74 for current and 0.81 for doubled CO_2 concentrations. Varying parameter and input variable values by ±10% resulted in a similar model response between morning and noon periods (less than or equal to 27.6% and 27.4%, respectively). Most parameters were more sensitive at noon than they were in the morning except for those that were correlated with air temperature, suggesting that air temperature has considerable influence over model sensitivity for these parameters/variables. Air temperature effect was greater under doubled than it was under current atmospheric CO_2 concentrations. In contrast, model sensitivity to CO_2 decreased under doubled CO_2 concentrations.

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1. Introduction

Photosynthetic models play a key role in simulating carbon flux and estimating net ecosystem production (NEP) when researching the terrestrial biosphere and CO_2 exchange between surface vegetation and the atmosphere (Sellers et al., 1997; Amthor et al., 2001; Hanson et al., 2004; Grant et al., 2005). These models represent not only the primary method for scientists to integrate small-scale process level phenomena into a comprehensive description of forest ecosystem structure and function, but also a key method for testing hypotheses concerning the response of forest ecosystems to changing environmental conditions. The CO_2 flux of an ecosystem is directly influenced by respiration and its pho-

* *Corresponding author*. Tel.: +1 514 987 3000x1056; fax: +1 514 987 4718.
E-mail address: peng.changhui@uqam.ca (C. Peng).
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tosynthetic capacity. Photosynthetic capacity is commonly simulated using mechanistic models while respiration is calculated using empirical functions from derived NEP. Since the late 1970s, a number of mechanistic-based models have been developed and used to simulate photosynthesis and respiration, providing a consistent description of carbon exchange between plants and the environment (Sellers et al., 1997). For most models, photosynthetic calculation of individual leaves is theoretically based upon (1) the biochemical formulations presented by Farquhar et al. (1980) and (2) the numerical solutions developed by Collatz et al. (1991). At the canopy level, the approach of "scaling-up" from leaf to canopy using Farquhar's model can be categorized into two types: "big-leaf" and "two-leaf" models (Sellers et al., 1996). The "two-leaf" treatment separates a canopy into sunlit and shaded portions (Kim and Verna, 1991; Norman, 1993; de Pury and Farquhar, 1997) and vertical integration against radiation gradient (Bonan, 1995).

Following the work of these pioneers, many studies have demonstrated the successful application of process-based carbon exchange models by improving model structure and parameterizing models for specific ecosystems (Tiktak and van Grinsven, 1995; Amthor et al., 2001; Hanson et al., 2004; Grant et al., 2005). For example, BEPS-InTEC (Liu et al., 1997; Chen et al., 1999), CLASS (Verseghy, 2000), ECOSYS (Grant, 2001), C-CLASSa (Wang et al., 2001), C-CLASSm (Arain et al., 2002), EALCO (Wang et al., 2002), and CTEM (Arora, 2003) are principle process-based models used in the Fluxnet-Canada Research Network (FCRN) for modelling NEP at an hourly or daily time step. However, these derivative and improved models usually require a large number of parameters and input variables that are in practice difficult to obtain and estimate when characterizing various forest stands and soil properties (Grant et al., 2005). The subsequent complexity of the results makes it difficult for modellers to perceptively understand model response to such large numbers of parameters and variables. Although many model parameterizations responsible for simulation biases were diagnosed and corrected for each individual site, it is still unclear how to resolve the differences among parameterizations for different sites and climate conditions. Additionally, different algorithms used for intermediate variables in a model usually affect model accuracy. For example, there are various considerations and approaches to consider for processing intercellular CO_2 concentrations (C_i) when calculating instantaneous CO_2 exchange. The key variable C_i is derived in various ways: (1) by using the empirical constant ratio of C_i to the atmospheric CO_2 concentration (C_a); (2) as a function of relative humidity, atmospheric CO_2 concentration and the species-specific constant (Kirschbaum, 1999) by eliminating stomatal conductance; (3) and by using a nested numerical convergence technique to establish an optimized C_i that meets the canopy energy balance of CO_2 and water exchange for a time point (Leuning, 1990; Collatz et al., 1991; Sellers et al., 1996; Baldocchi and Meyers, 1998). These approaches can significantly affect the accuracy and efficiency of a model. The effects of different algorithms on NEP estimation are therefore a great concern for model selection, influencing both the accuracy and efficiency of the model.

Moreover, the photosynthetic rate of fluctuation is highly correlated with daily cycles of radiation and temperature and, therefore, these cyclic ups and downs can be captured using

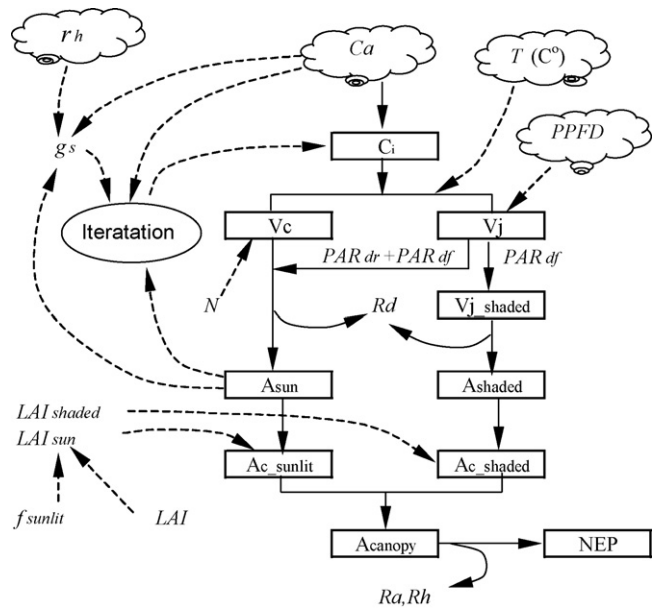

Fig. 1 – The structure of TRIPLEX-Flux. Rectangles represent key pools or state variables while ovals represent simulation processes. Solid lines represent carbon flows and the fluxes between the forest ecosystem and the external environment while dashed lines denote control and effects of environmental variables. A_{canopy} represents the sum of photosynthesis in the shaded and sunlit portion of the crowns, depending upon the outcome of V_c and V_j (see Table 1). $A_{c\,sunlit}$ and $A_{c\,shade}$ are net CO_2 assimilation rates for sunlit and shaded leaves. f_{sunlit} denotes the fraction of sunlit leaves in the canopy.

process-based carbon flux models (Amthor et al., 2001; Grant et al., 2005) and neural network approaches by training models to look for daily cycling events (Papale and Valentini, 2003). However, CO_2 flux is often underestimated during the day and overestimated at night, even when the frequency of alternation and diurnal cycling are simulated accurately. Amthor et al. (2001) compared nine process-based models to evaluate model accuracy and found that these models covered a wide range of complexity and approaches for simulating ecosystem processes. Annual CO_2 exchange, for example, was more variable between models within a year than it was between years for a given model. This means that differences between models and their parameterization characteristics are more important to the prediction of CO_2 exchange than interannual climatic variability. Grant et al. (2005) tested six ecosystem models to simulate the effects of air temperature and the vapor pressure deficit (VPD) on carbon balance. They suggested that the underestimate in some models of net carbon gain was attributed to an inadequate sensitivity of stomatal conductance to the VPD and eco-respiration to temperature. Their results show that there is a need to improve the ability of CO_2 flux simulation models on NEP estimation by recognizing how the structure and parameters of a model will influence model output and accuracy. Aber (1997) and Hanson et al. (2004) suggested that prior to the application of a given model for the purpose of simulation and prediction, appropriate documen-

Table 1 – Variables and parameters used in TRIPLEX-Flux to simulate an old black spruce site in the Boreal forest in Canada

Symbol	Unit	Description	Equation and value	Reference
A	$\mu mol\,m^{-2}\,s^{-1}$	Net CO_2 assimilation rate for big leaf	$A = \min(V_c, V_j) - Rd$ $A = g_s(C_a - C_i)/1.6$	Farquhar et al. (1980), Leuning (1990), Sellers et al. (1996)
A_{canopy}	$\mu mol\,m^{-2}\,s^{-1}$	Net CO_2 assimilation rate for canopy	$A_{canopy} = A_{sun}LAI_{sun} + A_{shade}LAI_{shade}$	Norman (1982)
A_{shade}	$\mu mol\,m^{-2}\,s^{-1}$	Net CO_2 assimilation rate for shaded leaf		
A_{sun}	$\mu mol\,m^{-2}\,s^{-1}$	Net CO_2 assimilation rate for sunlit leaf		
Γ	Pa	CO_2 compensation point without dark respiration	$\Gamma = 1.92 \times 10^{-4}O_2 1.75^{(T-25)/10}$	Collatz et al. (1991) and Sellers et al. (1992)
C_a	Pa	CO_2 concentration in the atmosphere	Input variable	
C_i	Pa	intercellular CO_2 concentration		
$f(N)$	–	Nitrogen limitation term	$f(N) = N/N_m = 0.8$	Bonan (1995)
$f(T)$	–	Temperature limitation term	$f(T) = (1 + \exp((-220{,}000 + 710(T + 273))/(R_{gas}(T + 273))))^{-1}$	Bonan (1995)
g_s	$m\,mol\,m^{-2}\,s^{-1}$	Stomatal conductance	$g_s = g_0 + m100Ar_h/C_a$	Ball (1988)
g_0	–	Initial stomatal conductance	57.34	Cai and Dang (2002)
m	–	coefficient	7.43	Cai and Dang (2002)
J	$\mu mol\,m^{-2}\,s^{-1}$	Electron transport rate	$J = J_{max}PPFD/(PPFD + 2.1J_{max})$	Farquhar and von Caemmerer (1982)
J_{max}	$\mu mol\,m^{-2}\,s^{-1}$	Light-saturated rate of electron transport in the photosynthetic carbon reduction cycle in leaf cells	$J_{max} = 29.1 + 1.64V_m$	Wullschleger (1993)
K	Pa	Function of enzyme kinetics	$K = K_c(1 + O_2/K_0)$	Collatz et al. (1991) and Sellers et al. (1992)
K_c	Pa	Michaelis–Menten constants for CO_2	$K_c = 30 \times 2.1^{(T-25)/10}$	Collatz et al. (1991) and Sellers et al. (1992)
K_0	Pa	Michaelis–Menten constants for O_2	$K_0 = 30000 \times 1.2^{(T-25)/10}$	Collatz et al. (1991)
M	$kg\,C\,m^{-2}$	Biomass density of each plant component	0.4 for leaf; 0.28 for sapwood; 1.4 for root	Gower et al. (1997), Kimball et al. (1997), Steele et al. (1997)
N	%	Leaf nitrogen content	1.2	Based on Kimball et al. (1997)
N_m	%	Maximum nitrogen content	1.5	Bonan (1995)
O_2	Pa	Oxygen concentration in the atmosphere	21,000	Chen et al. (1999)
PPFD	$\mu mol\,m^{-2}\,s^{-1}$	Photosynthetic photon flux density	Input variable	
Q_{10}	–	Temperature sensitivity factor	2.0	Goulden et al. (1998)
R_a	$kg\,C\,m^{-2}\,day^{-1}$	Autotrophic respiration	$R_a = R_m + R_g$	
r_a	–	Carbon allocation fraction	0.4 for root; 0.6 for leaf and sapwood	Running and Coughlan (1988)
R_d	$\mu mol\,m^{-2}\,s^{-1}$	Leaf dark respiration	$R_d = 0.015V_m$	Collatz et al. (1991)
R_e	$kg\,C\,m^{-2}\,day^{-1}$	Ecosystem respiration	$R_e = R_a + R_h$	
R_g	$kg\,C\,m^{-2}\,day^{-1}$	Growth respiration	$R_g = r_g r_a GPP$	Ryan (1991)
r_g	–	Growth respiration coefficient	0.25 for root, leaf and sapwood	Ryan (1991)
R_{gas}	$m^3\,Pa\,mol^{-1}\,K^{-1}$	Molar gas constant	8.3143	Chen et al., 1999
r_h	%	Relative humidity	Input variable	
R_h	$kg\,C\,m^{-2}\,day^{-1}$	Heterotrophic respiration	$R_h = 1.5Q_{10}^{(T-10)/10}$	Lloyd and Taylor, 1994

Table 1 (*Continued*)

Symbol	Unit	Description	Equation and value	Reference
R_m	$kg\,C\,m^{-2}\,day^{-1}$	Maintenance respiration	$R_m = Mr_m Q_{10}^{(T-T_0)/10}$	Running and Coughlan (1988) Ryan (1991)
r_m	–	Maintenance respiration coefficient	0.002 at 20 °C for leaf; 0.001 at 20 °C for stem; 0.001 at 20 °C for root	Kimball et al. (1997)
T	°C	Air temperature	Input variable	
V_c	$\mu mol\,m^{-2}\,s^{-1}$	Rubisco-limited gross photosynthesis rates	$V_c = V_m(C_i - \Gamma)/(C_i - K)$	Farquhar et al. (1980)
V_j	$\mu mol\,m^{-2}\,s^{-1}$	Light-limited gross photosynthesis rates	$V_j = J(C_i - \Gamma)/(4.5C_i + 10.5\Gamma)$	Farquhar and von Caemmerer (1982)
V_m	$\mu mol\,m^{-2}\,s^{-1}$	Maximum carboxylation rate	$V_m = V_{m25}0.24(T - 25)f(T)f(N)$	Bonan (1995)
V_{m25}	$\mu mol\,m^{-2}\,s^{-1}$	V_m at 25 °C, variable depending on vegetation type	45	Depending on Cai and Dang (2002)

tation of the model's structure, parameterization processes, sensitivity analysis, and testing of a model's output against independent observation must be conducted.

A series of sensitivity analyses were performed in this study to improve parameterization design in the development of ecosystem carbon flux models using TRIPLEX-Flux, a new canopy photosynthetic model developed on the earlier version of the TRIPLEX1.0 model (Peng et al., 2002) to simulate carbon exchange in Canada's Boreal forest ecosystems. TRIPLEX1.0 has been successfully calibrated and validated against age-dependent growth measurements from 12 permanent sample plots (PSP) for jack pine stands in northern Ontario (Peng et al., 2002), Boreal mixedwood stands in the Lake Abitibi Model Forest (Zhou et al., 2005, 2006) and other Boreal tree stands in BOREAS sites located in central Canada (Zhou et al., 2004). Unfortunately, TRIPLEX1.0 only operates on a monthly time step and is unable to simulate hourly and daily carbon fluxes and, therefore, unable to test model simulations again flux tower measurements. The major objectives of this study were: (1) to describe the new TRIPLEX-Flux model structure and features and to test model simulations against flux tower measurements and; (2) to examine and quantify the effects of model response to parameters, input variables and algorithms of the intercellular CO_2 concentrations and stomatal conductance calculations on ecosystem carbon flux. Analyses will have significant implications for the evaluation of factors that relate to gross primary productivity (GPP) as well as influence the outputs of a carbon flux model coupled with a two-leaf photosynthetic model.

2. Materials and methods

2.1. *Model development and description*

2.1.1. *Model structure*

TRIPLEX-Flux is designed to take advantage of the approach used in a two-leaf mechanistic model to describe the irradiance and photosynthetic capacity of the canopy as well as to simulate CO_2 flux in Boreal forest ecosystems. The model is composed of three parts: (1) leaf photosynthesis—the instantaneous gross photosynthetic rate is derived based upon the biochemical model of Farquhar et al. (1980) and the semi-analytical approach of Collatz et al. (1991), simulating photosynthesis using the concept of co-limitation by Rubisco (V_c) and electron transport (V_j). (2) Canopy photosynthesis—total canopy photosynthesis is simulated using de Pury and Farquhar's (1997) algorithm in which a canopy is divided into sunlit and shaded portions. The model describes the dynamics of abiotic variables such as radiation, irradiation, and diffusion. (3) Ecosystem carbon flux—the net ecosystem exchange (NEP) is modelled as the difference between photosynthetic carbon uptake and respiratory carbon loss (including autotrophic and heterotrophic respiration) and calculated using Q_{10} and a base temperature.

Fig. 1 illustrates the primary processes, outputs of the model and the control mechanisms. All parameters and their default values, variables, and functions used to calculate them are listed in Table 1. A_{canopy} is the sum of photosynthesis in the shaded and sunlit portions of the crowns depending on the outcome of V_c and V_j (see Table 1). $A_{c\,sunlit}$ and $A_{c\,shade}$ are the net CO_2 assimilation rates for sunlit and shaded leaves within the canopy, respectively.

The model runs at 30 min time steps and outputs carbon flux at different time intervals.

2.1.2. *Leaf photosynthesis*

Instantaneous leaf gross photosynthesis was calculated using Farquhar's model (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982). Simulation of this model consists of two components: the Rubisco-limited gross photosynthetic rate (V_c) and the light-limited (RuBP or electron transportation-limited) gross photosynthesis rate (V_j), expressed for C_3 plants as shown in Table 1. The minimum rate of the two is taken as the gross photosynthetic rate of the leaf without considering the sink limitation to CO_2 assimilation. The net CO_2 assimilation rate (A) is calculated by subtracting the leaf dark

respiration (Rd) from the above photosynthetic rate:

$$A = \min(V_c, V_j) - \mathrm{Rd} \quad (1)$$

This can also be further expressed using stomatal conductance and the difference in CO_2 concentration (Leuning, 1990):

$$A = g_s(C_a - C_i)/1.6 \quad (2)$$

The stomatal conductance can be derived in several different ways. The semi-empirical g_s model developed by Ball (1988) is used:

$$g_s = g_0 + 100\, mA\, r_h/C_a \quad (3)$$

All symbols in Eqs. (1)–(3) are described in Table 1. Since the intercellular CO_2 concentration C_i (Eqs. (1) and (2)) has a nonlinear response on the assimilation rate A, full analytical solutions cannot be obtained for hourly simulations. The iteration approach is used in this study to obtain C_i and A using Eqs. (1)–(3) (Leuning, 1990; Collatz et al., 1991; Sellers et al., 1996; Baldocchi and Meyers, 1998). To simplify the algorithm, the conservation equation for water transfer through stomata was not used. The stomatal conductance was calculated using a simple regression equation ($R^2 = 0.7$) developed by Cai and Dang (2002) based upon their experiments on black spruce:

$$g_s = 57.4 + 743\, A\, r_h/C_a \quad (4)$$

2.1.3. *Canopy photosynthesis*

In this study, the one-layer and two-leaf model was coupled to scale up the photosynthesis model from leaf to canopy, assuming that sunlit leaves receive both direct PAR (PAR_{dir}) and diffusive PAR (PAR_{dif}) while shaded leaves receive PAR_{dif} only. Estimating the mean leaf-sun angle at 60° for a Boreal forest canopy with spherical leaf angle distribution, the PAR received by sunlit leaves includes both PAR_{dir} and PAR_{dif} while the PAR for shaded leaves received PAR_{dif} only. Norman (1982) proposed an approach to calculate direct and diffuse radiation that can be used to run the numerical solution procedure (Leuning, 1990; Collatz et al., 1991; Sellers et al., 1996) for obtaining the net assimilation rate of sunlit and shaded leaves (A_{sun} and A_{shade}). With the separation of sunlit and shaded leaf groups, total canopy photosynthesis (A_{canopy}) is obtained as follows (Norman, 1981, 1993; de Pury and Farquhar, 1997):

$$A_{canopy} = A_{sun}\mathrm{LAI}_{sun} + A_{shade}\mathrm{LAI}_{shade} \quad (5)$$

where LAI_{sun} and LAI_{shade} are the leaf area indices for sunlit and shaded leaves, respectively; the calculation for LAI_{sun} and LAI_{shade} is described by de Pury and Farquhar (1997).

2.1.4. *Ecosystem carbon flux*

Net ecosystem production (NEP) is estimated by subtracting ecosystem respiration (R_e) from GPP (A_{canopy}):

$$\mathrm{NEP} = \mathrm{GPP} - R_e \quad (6)$$

where $R_e = R_g + R_m + R_h$. Growth respiration (R_g) is calculated based upon respiration coefficients and GPP while maintenance respiration (R_m) is calculated using the Q_{10} function multiplied by the biomass of each plant component. Both R_g and R_m are calculated separately for leaf, sapwood, and root carbon allocation fractions:

$$R_g = \sum (r_g r_a\, \mathrm{GPP}) \quad (7)$$

$$R_m = \sum (M\, r_m\, Q_{10}^{(T-T_0)/10}) \quad (8)$$

where r_g, r_a, r_m, and M represent adjusting coefficients and the biomass density for leaf, root, and sapwood, respectively (see Table 1). Heterotrophic respiration (R_h) is calculated by subtracting root respiration (r_m and r_g) from soil respiration (r_s), expressed as the exponential function of temperature and Q_{10} described by Lloyd and Taylor (1994) (see Table 1).

Table 2 – Site characteristics and stand variables

Site	BOREAS-NOBS: Northern Study Area, Old Black Spruce, Flux Tower, Manitoba, Canada
Latitude	55.88°N
Longitude	98.48°W
Mean January air temperature (°C)	−25.0
Mean July air temperature (°C)	+15.7
Mean annual precipitation (mm)	536
Dominant species	Black spruce *Picea mariana* (Mill.)
Average stand age (years)	160
Average height (m)	10.0
Leaf area index (LAI)	4.0

2.2. *Experimental data*

Flux tower data used for model testing and comparison were collected at an old black spruce (*Picea mariana* [Mill.] BSP) site in the Northern Study Area (FLX-01 NSA-OBS) of BOREAS (Nickeson et al., 2002) as well as from the latest version of BOREAS-NOBS (Dunn and Wofsy, 2007; Dunn et al., 2007). The average age of trees in the upland site was calculated at 160 years old and 10 m tall in 1993 (see Table 2). The site contained poorly drained silt and clay and 10% fen within 500 m of the tower (Chen et al., 1999). Further details concerning these sites and their measurements can be obtained from Sellers et al. (1997). Data used as model inputs included atmospheric CO_2 concentrations, air temperature, relative humidity, and photosynthetic photon flux density (PPFD). The 30-min NEP derived from tower and chamber measurements was compared to the model outputs (NEP).

3. Results and discussion

3.1. *Model validation*

Model validation was performed using the NEP data measured in the months of May, July, and September from 1994 to 1997 at the old black spruce BOREAS site. The simulation was compared with the observed NEP measurements at 30 min intervals for the month of July from 1994 to 1997 (Fig. 2). The

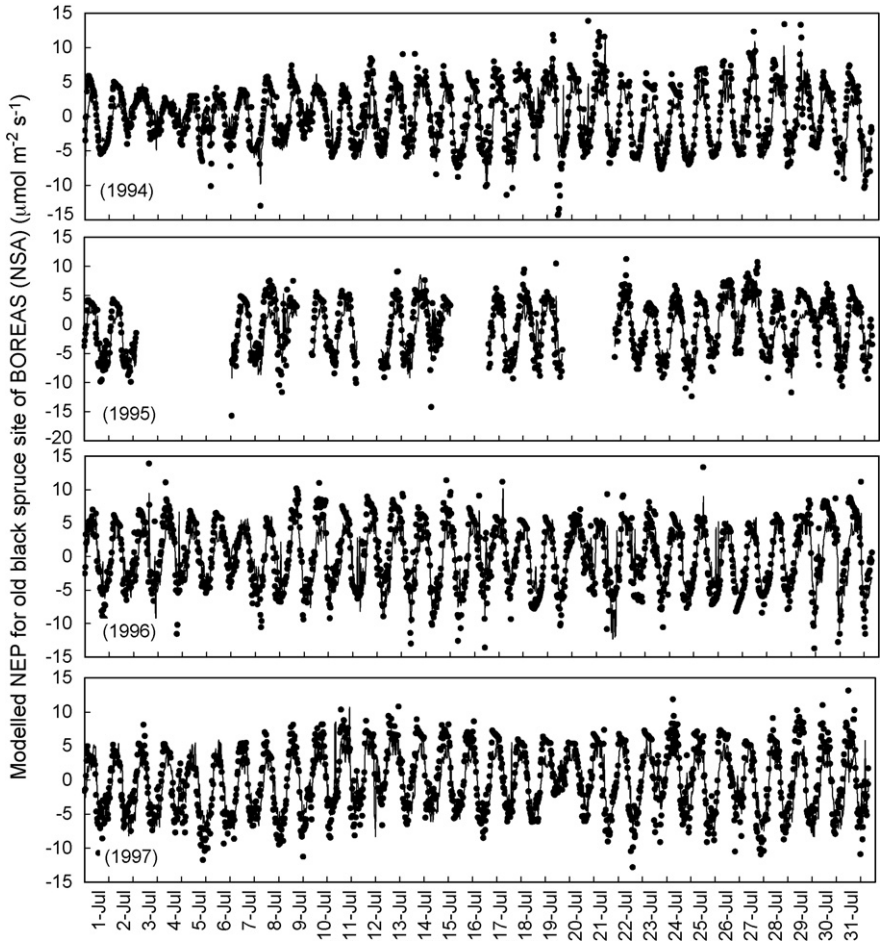

Fig. 2 – The contrast of hourly simulated NEP by TRIPLEX-Flux and observed NEP from the tower and chamber at an old black spruce BOREAS site for the month of July of 1994, 1995, 1996 and 1997. Solid dots denote measured NEP and solid lines represents simulated NEP. Discontinuance of dots and lines represent the missing measurements of NEP and associated climate variables.

simulated NEP and measured NEP are provided in a one-to-one relationship (Fig. 3) where $R^2 > 0.65$. Agreement between observations and predictions was good, suggesting that the parameterization of the model was consistent in contributing to realistic predictions. NEP patterns simulated by the model (solid line shown in Fig. 2) matched most observations (dots shown in Fig. 2); however, the TRIPLEX-Flux model failed to simulate some NEP peaks and valleys. For example, biases occur in particular on the 5th, 7th, 9th, 10th, and 11th of July, 1994 (peaks), and the 8th, 13th, 14th, 21st, and 22nd of July, 1994 (valleys). The differences between the model simulation and observations can be attributed not only to uncertainties and errors in flux tower measurements (Grant et al., 2005; see also the Sun et al. companion paper concerning this issue), but also to the model itself.

Because NEP is determined by both GEP and ecosystem respiration (R_e), it is necessary to verify the modelled GEP. Since GEP at this site cannot be measured by the flux tower, modelled GEP had to be compared with estimated GEE derived from observed NEE and estimated R_e (Fig. 4). The coefficient of determination (R^2) ranged from 0.67 to 0.76 for the month of July for the years 1994–1997. This implied that the structure and parameters of the model were correctly set for this particular site.

From a modelling point of view, bias usually results from two possible causes: when inconsequential model structure cannot take into account short-term changes in the environment and when the variation in the environment is not well captured due to poor model parameterization. To identify the reason for the bias in this study, variations of simulated NEP values were compared for all time steps with similar environmental conditions, such as atmospheric CO_2 concentrations, air temperature, relative humidity, and photosynthetic photon flux density (PPFD). Unfortunately, the comparison failed to pinpoint the cause of bias since similar environmental conditions may drive estimated NEP significantly higher or lower than the averages simulated by the model. This implies that the CO_2 flux model may require more input environmental variables than the four key variables used for the simulations. For example, soil temperature may cause respiration to change and, in turn, influence the amount of ecosystem respiration and the partition between root and heterotrophic respirations.

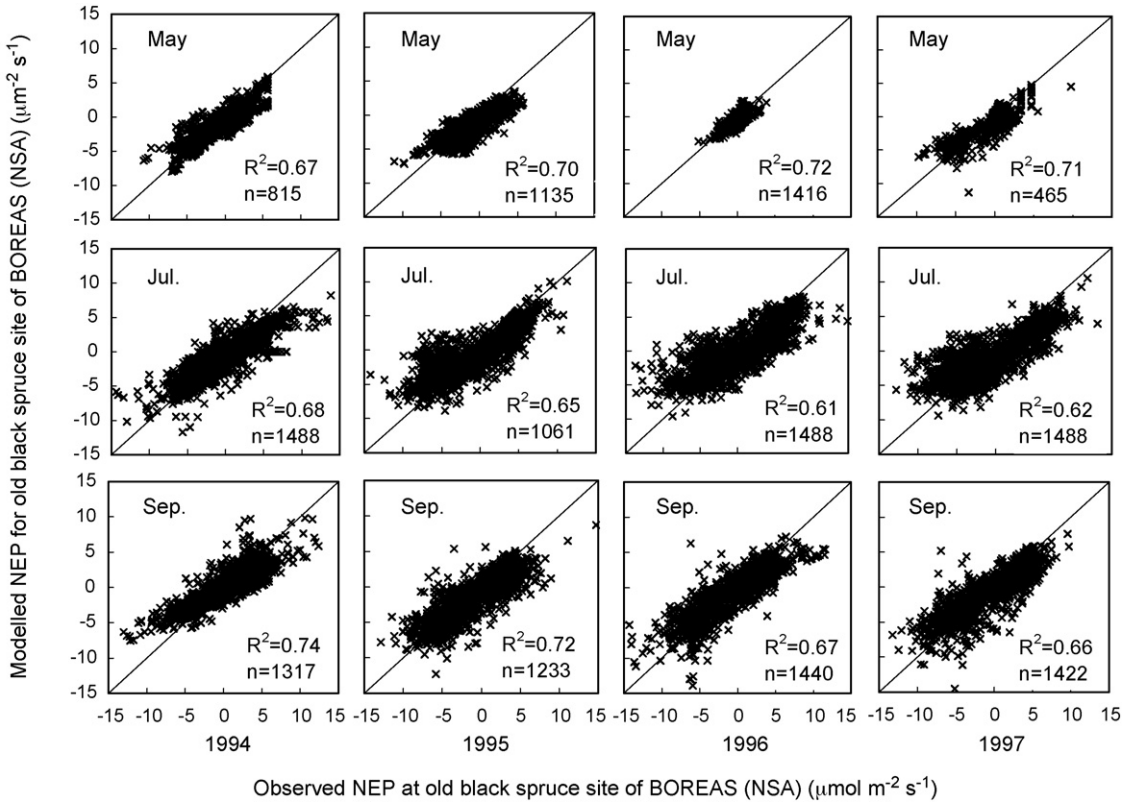

Fig. 3 – Comparisons (with 1:1 line) of hourly simulated NEP versus hourly observed NEP for the months of May, July and September of 1994, 1995, 1996 and 1997.

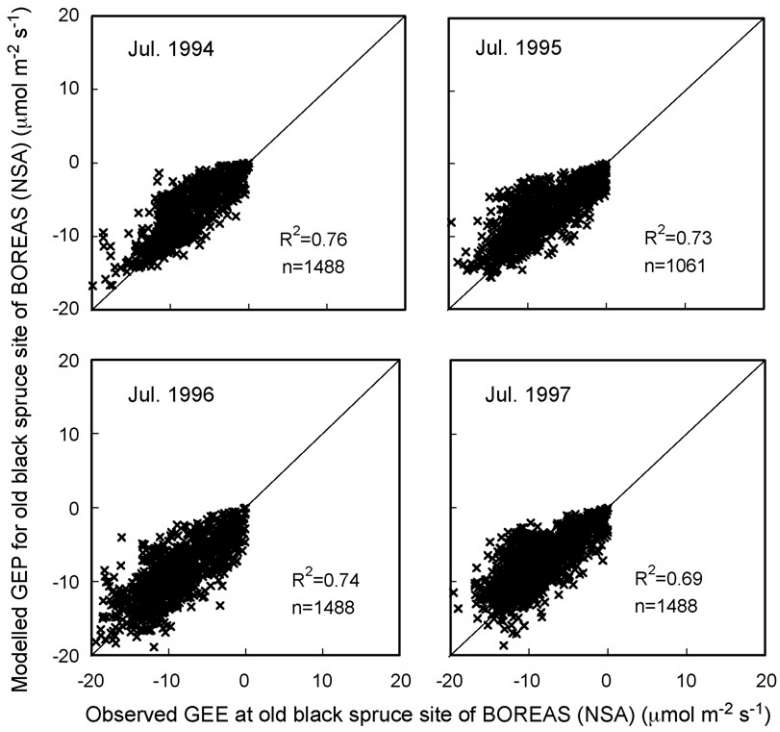

Fig. 4 – Comparisons of hourly simulated GEP versus hourly observed GEE for the month of July of 1994, 1995, 1996 and 1997, respectively.

Table 3 – Model inputs and responses used as a reference level in model sensitivity analysis

	$C_a = 360$		$C_a = 720$		Unit
	Morning	Noon	Morning	Noon	
Input					
C_a	360	360	720	720	ppm
T	15	25	15	25	°C
r_h	64	64	64	64	%
PPFD	680	1300	680	1300	$\mu mol\, m^{-2}\, s^{-1}$
Modelled					
NEP	0.14	0.22	0.19	0.34	$g\, C\, m^{-2}\, 30\, min^{-1}$
R_e	0.13	0.17	0.16	0.32	$g\, C\, m^{-2}\, 30\, min^{-1}$
LAI_{sh}/LAI_{sun}	0.56	1.44	0.56	1.44	–
$PPFD_{sh}/PPFD_{sun}$	0.25	0.23	0.25	0.23	–

LAI_{sun} and LAI_{sh} represent the leaf area indices for sunlit and shaded leaves; $PPFD_{sun}$ and $PPFD_{sh}$ denote the photosynthetic photon flux density for sunlit and shaded leaves. Morning and noon denote the time at 09:00 and 13:00 hours, respectively.

The empirical function (Eq. (3)) does not describe the relationship between soil respiration and other environmental variables with the exception of air temperature. Additionally, soil water could also influence simulated stomatal conductance (Tuzet et al., 2003), which may result in less assimilation under drought conditions despite more available irradiation (Xu et al., 2004). These are some of the factors that need to be considered in future versions of TRIPLEX-Flux. Additional testing and TRIPLEX-Flux applications applied to other Boreal tree species at different sites can be found in the Sun et al. companion paper (this issue).

3.2. *Sensitivity analysis*

Sensitivity analysis was conducted under two different climate conditions based on current atmospheric CO_2 concentrations and doubled CO_2 concentrations. Additionally, model sensitivity was tested and analyzed for both morning and noon periods. The four selected model input variables (lower C_a, T, r_h, and PPFD) are the averaged values at 0900 and 1300 hours. The higher C_a was set to 720 ppm and the air temperature was adjusted based upon the CGCM scenario that states that air temperature will increase up to approximately 3 °C by

Table 4 – Effects of parameters and inputs in model response to NEP

		$C_a = 360$		$C_a = 720$		Reference value
		Morning	Noon	Morning	Noon	
Parameters						
$f(N)$	+10%	8.7%	11.9%	4.9%	8.4%	See Table 1
	−10%	−14.5%	−15.7%	−8.6%	−10.3%	
Q_{10}	+10%	3.4%	−2.8%	1.4%	−1.7%	
	−10%	−3.4%	2.7%	−1.4%	1.7%	
r_m	+10%	−7.0%	−5.8%	−4.1%	−3.6%	
	−10%	0.9%	5.2%	1.4%	3.3%	
r_g	+10%	−5.9%	−6.4%	−5.6%	−5.3%	
	−10%	5.5%	5.7%	4.4%	4.8%	
r_a	+10%	<0.1%	<0.1%	<0.1%	<0.1%	
	−10%	<0.1%	<0.1%	<0.1%	<0.1%	
g_0	+10%	0.3%	<0.1%	<0.1%	<0.1%	
	−10%	<0.1%	<0.1%	<0.1%	<0.1%	
m	+10%	<0.1%	<0.1%	<0.1%	<0.1%	
	−10%	<0.1%	<0.1%	<0.1%	<0.1%	
Inputs						
C_a	+10%	7.4%	12.7%	1.9%	3.0%	See Table 3
	−10%	−9.9%	−14.7%	−2.4%	−4.0%	
T	+10%	2.6%	−8.3%	2.4%	3.5%	
	−10%	−3.3%	1.2%	−2.4%	−6.2%	
r_h	+10%	2.4%	<0.1%	0.5%	0.6%	
	−10%	−2.6%	<0.1%	−0.6%	−0.7%	
PPFD	+10%	1.0%	0.8%	2.4%	2.3%	
	−10%	−1.2%	−1.0%	−3.0%	−2.8%	

Morning and noon denote the time at 09:00 and 13:00 hours, respectively. Note that values of parameters and input variables were adjusted ±10% when testing model response.

Table 5 – Sensitivity indices for the dependence of the modelled NEP on selected model parameters and inputs

	$C_a = 360$		$C_a = 720$		Average
	Morning	Noon	Morning	Noon	
Parameters					
$f(N)$	1.16	1.38	0.68	0.93	1.04
r_g	0.57	0.60	0.50	0.50	0.54
r_m	0.39	0.55	0.28	0.35	0.39
Q_{10}	0.34	0.27	0.14	0.17	0.23
g_0	<0.1	<0.1	<0.1	<0.1	<0.1
m	<0.1	<0.1	<0.1	<0.1	<0.1
r_a	<0.1	<0.1	<0.1	<0.1	<0.1
Inputs					
C_a	0.90	1.38	0.22	0.35	0.37
T	0.35	0.48	0.24	0.49	0.25
PPFD	0.33	<0.1	0.27	0.26	0.19
r_h	0.33	<0.1	0.14	<0.1	0.13

Morning and noon denote the time at 09:00 and 13:00 hours, respectively. Sensitivity indices were calculated as ratios in the change (percentage) of model response to the given baseline of 20%.

the end of 21st century. Table 3 shows the various scenarios the model provided during the sensitivity analysis as well as modelled values to provide reference levels.

3.2.1. *Parameter testing*

Seven parameters were selected from the parameters listed in Table 1 for sensitivity analysis of the model. Since parameters vary considerably depending upon forest conditions, it is inherently difficult to determine parameters for different tree ages, sites, and locations. The selected parameters were considered critical for prediction accuracy of a CO_2 flux model based on a coupled photosynthetic model to simulate stomatal conductance, maximum carboxylation rate, and autotrophic and heterotrophic respiration. Table 4 summarizes the results of the sensitivity analysis of the model while Table 5 presents suggested sensitivity indices for model parameters and input variables. Each parameter in Table 4 was altered separately by increasing or decreasing its value by 10%. Model output sensitivity (NEP) is expressed as a change in percentage.

The modelled NEP varied in a direct consequence to the proportion of nitrogen limitation ($f(N)$), and changed in an indirect consequence or inversely to Q_{10} depending upon the time of the day (morning or noon) since the base temperature (20 °C) was between the morning temperature (15 °C) and noon temperature (25 °C) (Table 3). NEP varied inversely to parameter changes with the exception of r_a, g_0, and m that had little affect on model output (NEP). The response of model output to the ±10% parameter value change was less than 27.6% and generally greater under the current rather than the doubled atmospheric CO_2 concentration (Fig. 5). The simulation showed that increased CO_2 concentrations reduced the sensitivity of the model to the parameters. Therefore, CO_2 concentrations should be considered as a key factor when modelling NEP since they affect the level of sensitivity of the model to the parameters. Fig. 5 shows that the model is highly sensitive to $f(N)$, indicating that a greater effort should be made to improve the accuracy of $f(N)$ in order to increase the prediction accuracy of NEP using the TRIPLEX-Flux model.

3.2.2. *Model input variable testing*

Generally speaking, the response of the model to the input variables is of great significance during the model development phase since the response can be compared to other published or observed results at this stage to determine the reliability of the model. The sensitivity of the TRIPLEX-Flux model was tested to all input variables. Under the current atmospheric CO_2 concentration, C_a had greater effects than other input variables on the output of the model. By altering values of the input variables ±10%, the change in modelled NEP ranged from 17.3% to 27.6% at temperatures of 15 °C (morning) and 25 °C (noon) (Table 4 and Fig. 6). A 10% increase in atmospheric CO_2 concentration at noon only increased the NEP model output by 3%. In contrast to the greater impact of parameters, the effect of air temperature on NEP was greater under current rather than under doubled CO_2 concentrations. This may be related to the suppression of photorespiration by an increased CO_2 concentration. Thus, air temperature is likely a highly sensitive input variable at high atmospheric CO_2 concentrations. However, the current version of this model does not consider photosynthetic acclimation to CO_2 (downregulation or upregulation). Whether temperature will impact change when photosynthetic acclimation occur warrant further investigation. Fig. 7 shows the temperature response curve of the modelled NEP, illustrating the sensitivity of the

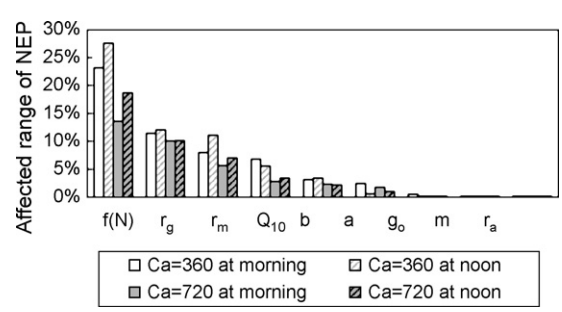

Fig. 5 – Variations of modelled NEP affected by each parameter as shown in Table 4. Morning and noon denote the time at 09:00 and 13:00 hours, respectively.

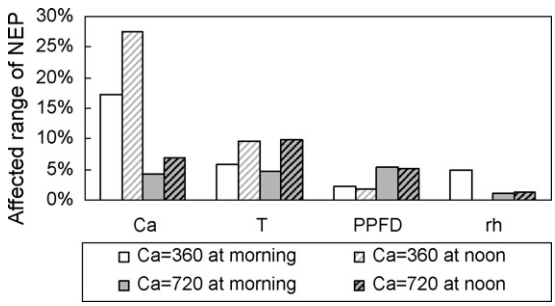

Fig. 6 – Variations of modelled NEP affected by each model input as listed in Table 4. Morning and noon denote the time at 09:00 and 13:00 hours, respectively.

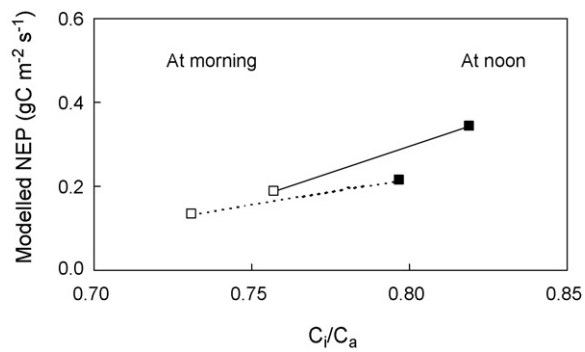

Fig. 8 – The response of NEP simulation using coupling the iteration approaches to the proportions of C_i/C_a under different CO_2 concentrations and timing. Open and solid squares denote morning and noon while dashed and solid lines represent current CO_2 and doubled CO_2 concentrations, respectively. Morning and noon denote the time at 09:00 and 13:00 hours, respectively.

output of the model to temperature changes within a range of temperatures. The curves peak at 20 °C under the current C_a and peak at 25 °C under the doubled C_a levels. The modelled NEP increased by approximately 57% from the current C_a at 20 °C to the doubled C_a at 25 °C. C_a sensitivity is close to the value (increased by approximately 60%) reported by McMurtrie and Wang (1993).

The effects of C_a and air temperature on NEP are greater than those of PPFD and relative humidity (r_h). In addition, C_a can also govern effects of r_h for specific times of day. For example, r_h affects NEP more during the morning than it does at noon for the current CO_2 concentration level (C_a = 360 ppm). Fig. 5 shows 6.1% variation of NEP in the morning and less than 0.1% at noon, suggesting a weak relationship between stomatal opening and r_h at noon. This is due to the stomata opening at noon where it reaches a maximal stomatal conductance, estimated at 300 mmol m^{-2} s^{-1} according to Cai and Dang's experiment (2002) of stomatal conductance for Boreal forests. In contrast, doubled CO_2 concentrations (C_a = 720 ppm) result in r_h always increasing above 0% (Fig. 5). This implies that

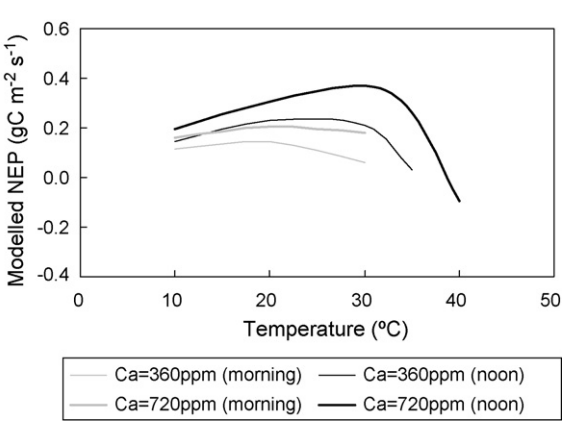

Fig. 7 – Temperature dependence of modelled NEP. Solid lines denote doubled CO_2 concentrations while dashed lines represent current air CO_2 concentration levels. The four curves represent different simulating conditions: current CO_2 concentrations in the morning (regular gray line) and at noon (bold gray line), and doubled CO_2 concentrations in the morning (regular black line) and at noon (bold black line). Morning and noon denote the time at 09:00 and 13:00 hours, respectively.

the stomata may not be completely opened at noon since an increasing CO_2 concentration leads to a significant decline of stomatal conductance, which reduces stomatal conductance by approximately 30% under doubled CO_2 concentration levels (Morison, 1987, 2001; Wullschleger et al., 2001; Talbott et al., 2003).

3.2.3. *Stomatal CO_2 flux algorithm testing*

Sensitivity analysis performed in this study included the examination of different algorithms for calculating intercellular CO_2 concentrations (C_i). Since stomatal conductance determines C_i at a given C_a, different algorithms of stomatal conductance affect C_i values and, in turn, affect the modelled NEP for the ecosystem. To simplify the algorithm, Wong et al. (1979) performed a set of experiments suggesting that C_3 plants tend to keep the C_i/C_a ratio constant. For this study, the response of this model was compared to two algorithms of C_i: the iteration algorithm and the ratio of C_i to C_a. The iteration algorithm resulted in a variation of the C_i/C_a ratio from 0.73 to 0.82 (Fig. 8). The C_i/C_a was lower in the morning than at noon and higher under the doubled than it was under current CO_2 concentrations. This range of variation agrees with Baldocchi's results that showed C_i/C_a ranging from 0.65 to 0.9 with modelled stomatal conductance ranging from 20 to 300 mmol m^{-2} s^{-1} (Baldocchi, 1994), but the values used for this study were slightly higher than Wong's experimental value of 0.7 (Wong et al., 1979). Results from this study suggest that a constant of the ratio (C_i/C_a) may not express realistic dynamics of the C_i/C_a ratio that is primarily determined by air temperature and relative humidity.

Generally speaking, stomatal conductance is affected by five environmental variables including solar radiation, air temperature, humidity, atmospheric CO_2 concentration, and soil water potential. The stomatal conductance model (iteration algorithm) used in this study unfortunately does not consider the effects of soil water. The Ball–Berry model (Ball, 1988) requires only A, r_h, and C_a as input variables; however, some investigations have argued that stomatal conductance

is dependent on the water vapor pressure deficit (Aphalo and Jarvis, 1991; Leuning, 1995) and transpiration (Mott and Parkhurst, 1991; Monteith, 1995) rather than r_h, especially under dry environmental conditions (de Pury, 1995).

By coupling the regression function (Eq. (3)) of stomatal conductance with the leaf photosynthesis model, g_0 and m described in Eq. (3) does not seem to affect NEP significantly. Although stomatal conductance is critical for governing exchanges between CO_2 and water, initial stomatal conductance (g_0) does not significantly affect stomatal conductance (g_s) if Ball's model is used. This implies that stomatal conductance (g_s) is primarily related to A, r_h, and C_a instead of g_0 and m. Thus, these two parameters measured from the black spruce site in northwestern Ontario (Cai and Dang, 2002) of the BOREAS region can be used instead for this study. Ball's model does not address some key variables to simulate stomatal conductance (g_s) like, for example, soil water. To improve model structure, the algorithm affecting model response must be considered for further testing the sensitivity of stomatal conductance by describing the effects of soil water potential for simulating the NEP of a Boreal forest ecosystem. Several models have been reported to have the ability to relate stomatal conductance to soil moisture. For example, Jarvis' model (Jarvis, 1976) contains a multiplicative function of photosynthetic active radiation, temperature, humidity deficits, molecular diffusively, soil moisture, and carbon dioxide. Similarly, the Mäkelä model (Mäkelä et al., 1996) has a photosynthesis and evaporation function. Finally, the ABA model (Triboulot et al., 1996) provides a function for leaf water potential. These models comprehensively consider major factors affecting stomatal conductance. Nevertheless, it is worthy to note that changing the stomatal conductance algorithm will impact the structure of the model. Since there is no feedback between stomatal conductance and internal CO_2 in the algorithm, it is debatable whether Jarvis' model is appropriate to be coupled within an iterative model.

4. Conclusion

We described the development and general structure of a simple process-based carbon exchange model, TRIPLEX-Flux, based upon well-tested representations of ecophysiological processes and the two-leaf mechanistic modelling approach. Model validation suggests that TRIPLEX-Flux is able to capture diurnal variations and patterns of NEP for an old black spruce site in central Canada, but failed to simulate peaks of NEP during the growing seasons from 1994 to 1997. Sensitivity analysis carried out for this study is critical to understand the relative roles of different model parameters in determining the dynamics of net ecosystem productivity. The nitrogen factor had the highest effect on modelled NEP (causing 27.6% variation at noon) while the autotrophic respiration coefficients showed intermediate sensitivity. Other factors were relatively low in terms of model response. The parameters used for the stomatal conductance function were not found to affect model response significantly. This raises an issue that needs to be clarified for future modelling work. Model inputs were also examined for sensitivity to model outputs. Modelled NEP is more sensitive to atmospheric CO_2 concentrations, resulting in a 27.4% variation of NEP at noon, followed by air temperature (e.g., 9.5% at noon), the photosynthetic photon flux density and relative humidity. Simulations showed different levels of sensitivity in the morning and at noon. Most parameters were more sensitive at noon than they were in the morning except those related to air temperature, such as Q_{10} and the coefficients for the regression function of soil respiration. Results suggest that air temperature had considerable effect on the sensitivity of these temperature-dependent parameters. Under the assumption of doubled CO_2 concentrations, the sensitivity of modelled NEP decreased for all parameters and increased for most model input variables except for atmospheric CO_2 concentrations. This implies that temperature related factors are crucial and more sensitive than other factors used in modelling ecosystem NEP when atmospheric CO_2 concentrations increase. Additionally, model validation suggests that more input variables would be helpful for improving model performance and prediction accuracy.

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