

Approaches for reducing uncertainties in regional forest carbon balance

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Abstract. Accurate estimation of regional terrestrial ecosystem carbon (C) balance is critical in formulating national and global adaptation and mitigation strategies in response to global changes. Since the regional C balance cannot be measured directly, it has been estimated using various models. In such studies, errors often exceeded the magnitude of the estimated C balance due to two types of uncertainties: noninclusion of some important factors in the C cycle and the fact that the C balance is a small difference between several large fluxes that can each be determined with only a limited accuracy. In this study, we propose new approaches to reduce these uncertainties and implement them in an Integrated Terrestrial Ecosystem C-budget model (InTEC). To minimize the first type of uncertainties, InTEC considers all the major factors presently known to affect C balance (including climate, atmospheric CO₂ concentration, N deposition, and disturbances). To reduce the second type of uncertainties, InTEC estimates the C balance from historical changes in these factors, relative to the preindustrial period. InTEC is built on the basis of widely tested Century C cycling model, Farquhar's leaf photosynthesis model, and age-NPP relationships, and is constrained by N cycling. As a general regional-scale terrestrial ecosystem C budget model, InTEC has so far been applied to Canada's forests [Chen *et al.*, this issue]. The sensitivity analysis showed that these two new approaches reduce the uncertainty in the C balance of Canada's forests substantially.

1. Introduction

Global carbon (C) budget studies have suggested that terrestrial ecosystems may be responsible for the "missing sink" of $\sim 2 \text{ Pg C yr}^{-1}$ ($1 \text{ Pg} = 10^{15} \text{ g}$) [Ciais *et al.*, 1995]. This missing sink is an order of magnitude larger than the emission reduction targets set in the Kyoto Protocol, i.e., the commitment that 38 industrialized nations made to reduce fossil fuel C emission by 5.2% on average from 1990 levels during the period 2008-2012. A better understanding of the spatial distribution and temporal variation of the missing sink has therefore significant implications not only on the global C balance but also on environmental and economic policies. Because of high C storage capacity and long C residence time, forest ecosystems, especially those at northern middle to high latitudes, are believed to be the most likely candidate for the missing sink.

While estimates of a regional forest C balance can be obtained using various modeling approaches and data, large uncertainties often exist in these estimates owing to two types of error. The first type is caused by the omission of some important factors owing to data limitations or assumptions about the importance of individual factors [Greenough *et al.*, 2000]. For example, the C balance of forest ecosystems has been studied on the basis of age-class distributions as affected

by disturbances such as forest fire, insect-induced mortality, and harvest [Kolchugina and Vinson, 1993; Turner *et al.*, 1995]. Other researchers have found that the effects of CO₂ fertilization, climate variability, and nitrogen (N) deposition could be substantial [Houghton *et al.*, 1996]. While studies that consider selected factors are useful for better understanding of their roles in C balance, to regard the resulting estimates as a full C balance of a region is incomplete and potentially misleading. The second type error is due to the fact that the C balance is a small difference between several large fluxes that can each be measured or estimated with a limited accuracy. For example, if the global terrestrial C sink is estimated as the difference between global net primary productivity (NPP) of 50-60 Pg C yr⁻¹ and corresponding heterotrophic respiration R_h , a 10% error in NPP will result in a 5-6 Pg C yr⁻¹ uncertainty in the global C balance even if R_h is determined perfectly. This uncertainty is 2-3 times larger than the missing sink.

In this study, we propose new modeling approaches that aim to reduce the above uncertainties. It is implemented through an Integrated Terrestrial Ecosystem C-budget model (InTEC), which couples the widely tested Century soil C cycling model [Parton *et al.*, 1987; Schimel *et al.*, 1996] and Farquhar's leaf photosynthesis model [Farquhar *et al.*, 1980; Bonan, 1995; Luo *et al.*, 1996]. InTEC is a general regional-scale terrestrial ecosystem C budget model, and has been applied to Canada's forests [Chen *et al.*, this issue]. For this specific application we calibrate parameters in the model using data from Canada's forests. In the final sensitivity analysis section we show why the uncertainties in the C

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balance of Canada's forests can be reduced by implementing the new approaches in InTEC.

2. New Modeling Approaches in InTEC

A regional forest C budget model usually involves C pools that store C, C fluxes that transfer C between pools, and factors that affect C fluxes and consequently the size of pools. To reduce the first type of uncertainties, it is essential to consider all major C pools, C fluxes, and the factors in a regional C budget model. Although this approach is straightforward in principle, its implementation can be difficult because of limitations both in data availability and in our knowledge of processes involved. For example, it has been a challenge to incorporate the effects of climate, CO₂, and N deposition into age-class-based modeling approach [Kurz et al., 1992].

The annual C balance of forest ecosystems and products in year *i*, $dC(i)/di$, equals the summation of fluxes between C pools and the atmosphere while interpool C fluxes cancel mutually:

$$\frac{dC(i)}{di} = NPP(i) - \frac{\xi A_f(i)}{A_t} - K(i)C(i), \tag{1}$$

where ξ is the C emission per unit burned forest area, $A_f(i)$ is the burned area in year *i*, A_t is the total forest area, $K(i)$ is the

weighted C transfer coefficient between C pools and the atmosphere and is given by $\{A(i)[K_{cd,a}C_{cd}(i) + K_{cf,a}C_{cf}(i) + K_{md,a}C_{md}(i) + K_{m,a}C_m(i) + K_{s,a}C_s(i) + K_{pa,a}C_p(i)] + K_{fu,a}C_{fu}(i) + K_{pa,a}C_{pa}(i) + K_{lo,a}C_{lo}(i)\}/C(i)$, and $C(i)$ is the total C content in biomass, soil, and forest product pools. The second term in the right hand side of (1) represents the area-averaged C emission due to fire, and the third term represents the sum of soil respiration and forest product oxidation. To reduce the second type of uncertainties, the values of NPP, fire C emission, and soil respiration and forest product oxidation should not be calculated independently. Instead, we propose a historical change approach which assumes that the C and N exchanges between terrestrial ecosystems and the atmosphere were in equilibrium under the mean conditions of climate and atmospheric chemistry and mean disturbance rate during the pre-industrial period. Solving (1) for $C(i)$ and taking its derivative with respect to time *t*, we have

$$\frac{dC(i)}{di} = NPP(i) - \frac{\xi A_f(i)}{A_t} - K(i)e^{-\sum_{j=0}^i K(j)} \{C(0) + \sum_{j=0}^i [NPP(j) - \frac{\xi A_f(j)}{A_t}] e^{\sum_{k=0}^j K(k)}\}. \tag{2}$$

Under the mean conditions of climate and atmospheric chemistry and mean disturbance rate during the preindustrial

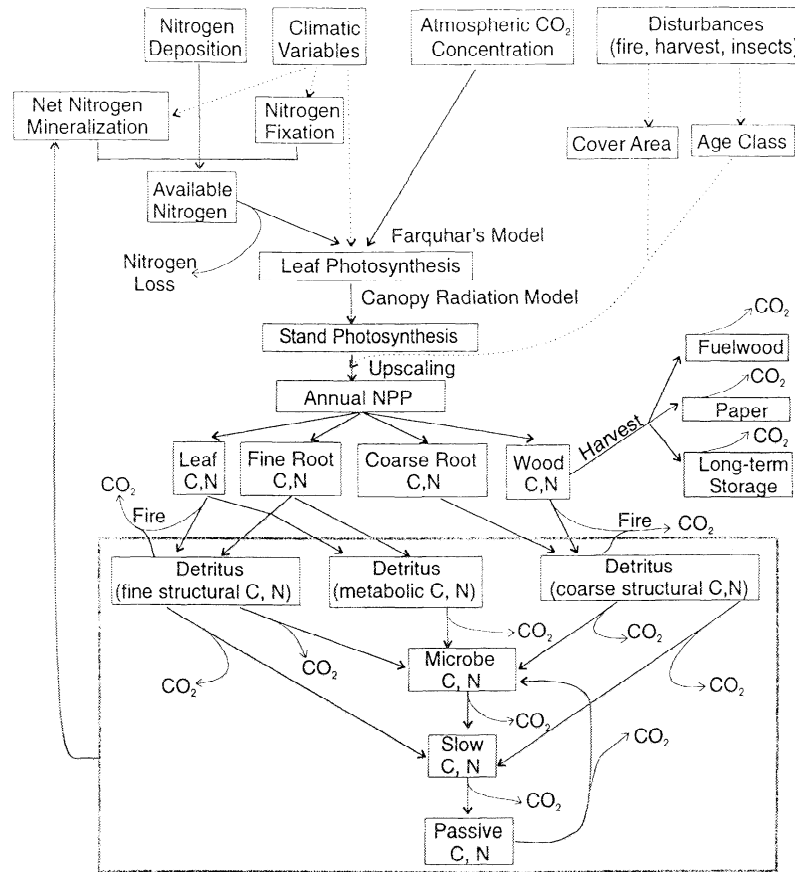


Figure 1. Structure of an integrated terrestrial ecosystem C-budget model (InTEC), which synthesizes the interactive effects of disturbances, nitrogen deposition, climate change, and CO₂ fertilization on the C budget of boreal forests. Dashed arrows indicate influences, and solid arrows show C-N flows.

Table 1. Coefficients of Carbon Allocation to Biomass Components, Coefficients of C Transfer Between C Pools, and Mean C Release Per Unit Burned Forest Area

Symbol	Value	Unit	References
f_w	0.38	dimensionless	1, 2, 3, 4
f_{cr}	0.11	dimensionless	1, 2, 3, 4
F_l	0.23	dimensionless	1, 2, 3, 4
f_{fr}	0.28	dimensionless	1, 2, 3, 4
$k_{w,cd} \times 10^{-3}$	27.8	year ⁻¹	5, 6, 9
$k_{cr,cd} \times 10^{-3}$	44.8	year ⁻¹	5, 6, 9
$k_{l,cmd} \times 10^{-3}$	294.8	year ⁻¹	5, 6, 9
$k_{fr,cmd} \times 10^{-3}$	594.8	year ⁻¹	5, 6, 9
$k_{cd,a} \times 10^{-3}$	13.3	year ⁻¹	5, 6
$k_{cd,m} \times 10^{-3}$	6.0	year ⁻¹	5, 6
$k_{cd,s} \times 10^{-3}$	14.0	year ⁻¹	5, 6
$k_{rd,a} \times 10^{-3}$	37.8	year ⁻¹	5, 6
$k_{rd,m} \times 10^{-3}$	17.1	year ⁻¹	5, 6
$k_{rd,s} \times 10^{-3}$	39.7	year ⁻¹	5, 6
$k_{md,a}$	0.6	year ⁻¹	5, 6
$k_{md,m}$	0.4	year ⁻¹	5, 6
$k_{m,a} \times 10^{-3}$	102.4	year ⁻¹	5, 6
$k_{m,s} \times 10^{-3}$	83.8	year ⁻¹	5, 6
$k_{m,p} \times 10^{-3}$	5.0	year ⁻¹	5, 6
$k_{s,a} \times 10^{-3}$	12.1	year ⁻¹	5, 6
$k_{s,p} \times 10^{-3}$	0.3	year ⁻¹	5, 6
$k_{p,a} \times 10^{-3}$	0.15	year ⁻¹	5, 6
$k_{p,m} \times 10^{-3}$	0.13	year ⁻¹	5, 6
ξ_w	650	g C m ⁻² yr ⁻¹	7, 8
ξ_{cd}	380	g C m ⁻² yr ⁻¹	7, 8
ξ_l	100	g C m ⁻² yr ⁻¹	7, 8
ξ_{fd}	190	g C m ⁻² yr ⁻¹	7, 8

References: 1, King et al. [1997]; 2, Townsend et al. [1996]; 3, Gower et al. [1997]; 4, Steele et al. [1997]; 5, Schimel et al. [1994]; 6, Schimel et al. [1996]; 7, Kurz et al. [1992]; 8, Bonan [1990]; 9, estimation made in this study.

period, $C(0) = [NPP(0) - \xi_{A_f}(0)]/K(0)$. The C balance in a given year is thus determined by NPP, K , and ξ_{A_f} during all years since the industrialization.

These approaches are implemented in InTEC (Figure 1). Four biomass C pools (i.e., wood, leaf, coarse root, and fine root), six soil C pools (coarse structural detritus, fine structural detritus, metabolic detritus, microbe, slow, and passive), and three forest product C pools (into fuelwood, paper products, and long-term storage) are considered in InTEC, following Schimel et al. [1996] and Houghton [1993]. The C allocation coefficients from NPP to biomass pools are given in Table 1. A fraction of the biomass is transferred into soil and products C pools through litterfall, forest self-thinning, and disturbances (including fire, insect-induced mortality, and harvest). Although fires release C directly and climate changes affect soil respiration, the effects of N deposition, climate, atmospheric CO₂, and disturbances on C balance are incorporated mainly through their effects on NPP. Along with the C cycling, N cycling in the soil determines the amount of N in soil available for uptake by plants and so acts as a feedback to NPP. Sections 2.1-2.3 describe the model in detail.

2.1. Carbon Cycling

The equations for describing C cycling processes in InTEC are similar to the well-tested Century model [Schimel et al., 1996], except the following four modifications. (1) The soil structural C pool is divided into coarse and fine components to better characterize forest detritus. (2) Disturbance effects are considered in InTEC. Fires emit large fractions of biomass and detritus C into the atmosphere and return a fraction of unburned biomass to soil. Insect-induced mortality returns all biomass to soil, while harvest transfers a fraction of wood to product pools and the remainder to soil. (3) Instead of using a constant Q_{10} to calculate the abiotic decomposition factor A , we use a modified Arrhenius-type equation of Lloyd and Taylor [1994] (further discussion is given in section 3). (4) Probably most importantly, we calculate the NPP using the process-based leaf photosynthesis model [Farquhar et al., 1980; Sellers et al., 1992; Bonan, 1995; Luo et al., 1996; J.M. Chen et al., 1999]. Although the Farquhar model has been well tested at short time scale, its application at longer timescale needed proper constraints and scaling up [Restetter et al., 1996]. With respect to long-term C uptake patterns, the nutrient constraints, especially N in middle and high-latitude forest ecosystems, are the most important. We discuss N cycling in section 2.2 and a new scaling-up algorithm in section 2.3.

2.2. Nitrogen Cycling

We describe the N cycling in forest ecosystems using an approach similar to that of Townsend et al. [1996] and Holland et al. [1997], except for following three aspects. (1) In InTEC the C/N ratios of biomass are allowed to vary on the basis of the amount of N uptake and NPP, instead of being a constant as assumed by the above authors. The C/N ratios of soil C pools vary as litterfall with different C/N ratio enters the soil C pools, except for those of microbe and passive soil C pools. Experimental evidence showed that C/N ratios of biomass and soil C pools vary from year to year [Schimel et al., 1994] and with different N and CO₂ levels [Pregitzer et al., 1995]. The later version of Century [Schimel et al., 1996] and other recent C-N cycling models [e.g., Comins, 1997] have also incorporated the changes in C/N ratios. (2) While Townsend et al. [1996] used a prescribed ratio for N loss and N uptake, we calculate the N uptake using a Michaelis-Menten relationship and assume the N loss is linearly proportional to soil N concentration [see also Rastetter et al., 1991; Hudson et al., 1994]. In the cases of long-term high N deposition rate and high-dose N fertilizer application the N uptake rate will become saturated, and so the ratio of N uptake to available N will be reduced dramatically. (3) We calculate NPP using Farquhar's leaf photosynthesis model, while Townsend et al. [1996] estimated the C input from the N uptake and C/N ratio. The N fixation rate is determined on the basis of the work of Chapin and Bledsoe [1992]. A measured N deposition rate is used in the study.

2.3. Annual Regional NPP Since Preindustrial Period

The area-averaged annual NPP is the most important input into the above C-N cycles. To estimate these NPP values, we first calculate the area-averaged annual gross photosynthesis

rate of a forest region in year i , $P(i)$, given by integrating the photosynthesis rate for all leaves (x) over the whole forest region (y) and time periods during the year (t)

$$P(i) = \frac{1}{A_i} \int_t \int_y \int_x p(x, y, t) dx dy dt, \quad (3)$$

where $p(x, y, t)$ is the instantaneous photosynthesis rate of a single leaf. For C_3 plants, which include all boreal forest species, $p(x, y, t)$ is limited by the minimum of [Farquhar et al., 1980; Luo et al., 1996]:

$$p_1 = J \frac{c_i - \Gamma}{4.5c_i + 10.5\Gamma}, \quad (4)$$

$$p_2 = V_m \frac{c_i - \Gamma}{c_i + k_{co}}$$

where p_1 and p_2 are leaf gross photosynthesis limited by electron transport and rubisco activity, respectively. The meaning of other terms in (4) is given in the notation list, and formulae for these terms are adopted from Sellers et al. [1992] and Bonan [1995].

There are many ways to scale leaf photosynthesis up to canopy photosynthesis [Norman, 1993]. Among these, a simple yet effective approach is to stratify canopy into sunlit and shaded leaves [Norman, 1993]. This is because T_a , c_a , and VPD are similar for all leaves within a canopy due to canopy air generally being well mixed during daytime. The sunlit-shaded stratification is important given that irradiation varies greatly for different leaves depending on their relative positions to the sun, resulting in different J values. With this stratification and canopy radiation models [Black et al., 1991; J.M. Chen et al., 1999] we calculate instantaneous canopy photosynthesis rate, p_{can} , as the minimum of

$$p_{can1} = (J_{sun} LAI_{sun} + J_{shad} LAI_{shad}) \frac{c_i - \Gamma}{4.5c_i + 10.5\Gamma}, \quad (5)$$

$$p_{can2} = V_m \frac{c_i - \Gamma}{c_i + k_{co}} LAI_l.$$

Assuming f_p is the fraction of canopy photosynthesis determined by p_{can1} , we calculate the canopy photosynthesis rate over the time period by

$$p_{can} = f_p p_{can1} + (1 - f_p) p_{can2}. \quad (6)$$

The above scaling procedure from a single leaf to a canopy thus reduces equation (3) to

$$P(i) = \frac{1}{A_i} \int_t \int_y p_{can}(y, t) dx dt. \quad (7)$$

While it is theoretically possible to calculate $P(i)$ for each year from 1895 to now, such an operation is practically limited by data availability and computation demand. An alternative is to calculate $P(i)$ only for a recent year for which quality data are available, and to determine $P(i)$ in other years using a relationship between the interannual relative change in $P(i)$, i.e., $(dP(i)/[P(i)di])$, and the main driving factors. Differentiating (7), we have

$$\frac{dP(i)}{di} = \int_t \int_y \frac{dp_{can}(y, t)}{A_i} dy dt + \int_t \frac{p_{can}(y, t)}{A_i} \frac{\partial y}{\partial i} dy + \int_y \frac{p_{can}(y, t)}{A_i} \frac{\partial t}{\partial i} dy, \quad (8)$$

where term 1 in the right hand side of (8) represents the effect on $dP(i)/di$ caused by changes in $p_{can}(y, t)$, while terms 2 and 3 represent, respectively, the effects caused by the changes in forest cover area and by the growing season length l_g . The value of $dp_{can}(y, t)$ is obtained by differentiating (6):

$$dp_{can}(y, t) = f_p p_{can1}(y, t) [L_1 dc_a + L_{N1} dN_l + (L_{T1,1} + L_{T1,2} + L_{T1,3}) dT_a] + (1 - f_p) p_{can2}(y, t) [L_2 dc_a + L_{N2} dN_l + (L_{T2,1} + L_{T2,2} + L_{T2,3} + L_{T2,4}) dT_a], \quad (9)$$

where L_1 , L_2 , $L_{T1,1}$, $L_{T1,2}$, $L_{T1,3}$, L_{N1} , $L_{T2,1}$, $L_{T2,2}$, $L_{T2,3}$, $L_{T2,4}$, and L_{N2} are coefficients for the effects of CO_2 fertilization, climate variability, and N availability (appendix). Due to the lack of data about changes in h_r , S_{sun} , S_{shad} , LAI_{sun} , LAI_{shad} , and LAI_l from the pre-industrial period to the present, we omit their impacts in this study. Since L_x and p_{can} vary diurnally and seasonally as well as among locations, L_x and p_{can} cannot be factored out of the two-dimensional integration in (8). Consequently, detailed data for coefficients and canopy photosynthesis rates are required for this integration. In reality, this is impossible, especially for the long historical periods in this study. To avoid this difficulty, we use a three-step spatial and temporal scaling algorithm. (1) We replace the integration by a discrete summation. (2) We estimate the discrete summation using the concept of correlation coefficient r , between the two variables L_x and p_{can} , namely,

$$\sum_{j=1}^n L_x(i, j) p_{can}(i, j) = n \overline{L_x(i)} \overline{p_{can}(i)} + \frac{r(i) \sigma_{L_x}(i) \sigma_{p_{can}}(i)}{n \overline{L_x(i)} \overline{p_{can}(i)}} = n \overline{L_x(i)} \overline{p_{can}(i)} + \zeta_{L_x, p_{can}}(i),$$

where n is the number of data points which can be time periods and spatial locations numbered by j , $\overline{L_x(i)}$ is the spatial and temporal ensemble average of L_x in year i , and σ is the standard deviation. (3) The ensemble average $\overline{L_x(i)}$ may differ significantly from that calculated using annual mean value of climate, N availability, and CO_2 concentration (i.e., $\overline{L_x(i)}$). Yet, because of limited data availability, it is more desirable to calculate $\overline{L_x(i)}$. For this purpose we introduce a conversion coefficient ψ_{L_x} ($= \overline{L_x(i)} / \overline{L_x(i)}$). Using this formulation, we calculate term 1 of (8) as follows:

$$\int_t \int_y \frac{dp_{can}(y, t)}{A_i} dy dt = f_p \left[\frac{P(i) + P(i-1)}{2} \right] [\zeta_{L_1, p} \psi_{L_1} \overline{L_1}(i) \Delta c_a(i) + \zeta_{L_{T1,1}, p} \psi_{T1,1} \overline{L_{T1,1}}(i) \Delta T_a(i) + \zeta_{L_{T1,2}, p} \psi_{T1,2} \overline{L_{T1,2}}(i) \Delta T_a(i) + \zeta_{L_{T1,3}, p} \psi_{T1,3} \overline{L_{T1,3}}(i) \Delta T_a(i) + \zeta_{L_{N1}, p} \psi_{N1} \overline{L_{N1}}(i) \Delta N(i)] + (1 - f_p) \left[\frac{P(i) + P(i-1)}{2} \right] [\zeta_{L_2, p} \psi_{L_2} \overline{L_2}(i) \Delta c_a(i) + \zeta_{L_{T2,1}, p} \psi_{T2,1} \overline{L_{T2,1}}(i) \Delta T_a(i) + \zeta_{L_{T2,2}, p} \psi_{T2,2} \overline{L_{T2,2}}(i) \Delta T_a(i) + \zeta_{L_{T2,3}, p} \psi_{T2,3} \overline{L_{T2,3}}(i) \Delta T_a(i) + \zeta_{L_{T2,4}, p} \psi_{T2,4} \overline{L_{T2,4}}(i) \Delta T_a(i) + \zeta_{L_{N2}, p} \psi_{N2} \overline{L_{N2}}(i) \Delta N(i)] = \mathcal{X}_1(i) \left[\frac{P(i) + P(i-1)}{2} \right]. \quad (10)$$

Term 2 in the right hand side of (8) represents the effect of change in forest area on the total photosynthesis.

Disturbances (e.g., forest fire, clear-cut harvest, and insect-induced forest mortality) can cause temporary changes in forest area. We include the changes in forest area due to these disturbances into disturbance effects. The effect of permanent changes in forest area due to land use change is given by

$$\int_t^{\infty} \frac{P_{\text{can}}(y,t)}{A_t} \frac{\partial y}{\partial i} dt = \frac{P(i) + P(i-1)}{A_t(i) + A_t(i-1)} \Delta A_t(i) = \chi_2(i) \frac{P(i) + P(i-1)}{2}. \quad (11)$$

Term 3 in the right hand side of (8) is the result of growing season length change, i.e.,

$$\int_y^{\infty} \frac{P_{\text{can}}(y,t)}{A_t} \frac{\partial t}{\partial i} dy = \frac{P(i) + P(i-1)}{l_g(i) + l_g(i-1)} \Delta l_g(i) = \chi_3(i) \frac{P(i) + P(i-1)}{2}. \quad (12)$$

This term can be very important in high latitudes where growing season is short and air temperature has increased at higher rates than at low and middle latitudes [Frolking, 1997; W.J. Chen *et al.*, 1999]. Inserting equations (10)-(12) into (8), we calculate the interannual relative change in $P(i)$ by

$$\frac{dP(i)}{di} = [\chi_1(i) + \chi_2(i) + \chi_3(i)] \left[\frac{P(i) + P(i-1)}{2} \right] = \chi(i) \left[\frac{P(i) + P(i-1)}{2} \right]. \quad (13)$$

So far, we have considered only the gross photosynthesis rate. Depending on plant species, NPP is only ~25% to 60% of the gross photosynthesis rate $P(i)$ because a large part is consumed by autotrophic respiration [Ryan *et al.*, 1997]. However, the ratio of NPP to $P(i)$ is conservative with climate change and N status [Ryan *et al.*, 1997], i.e., $dNPP(i)/NPP(i)di = dP(i)/P(i)di$. Therefore NPP affected by non-disturbance factors NPP_u can then be calculated as:

$$NPP_u(i) = NPP_u(0) \prod_{j=1}^i \frac{2 + \chi(j)}{2 - \chi(j)}. \quad (14)$$

With one known NPP in a calibration year and calculated $\chi(i)$, values of NPP for all other years can be calculated using (14).

Disturbances affect NPP through altering age-class distribution and forest area. The age distribution of forest stands in a given year, $A(y,i)$, can be estimated from historical disturbance records, the length of regeneration period, and the rate of survival after regeneration:

$$A(y,i) = A_t \frac{q(i)}{\varphi(1/s + 1)} e^{-[q(i)y]^s}, \quad (15)$$

where q is the total fire and insect occurrence frequency, φ is the gamma function, and s is the shape parameter [Kasischke *et al.*, 1995]. At $y = 0$ (i.e., for area disturbed and yet not regenerated) the area is the sum of disturbed areas in previous n years, where n is the average number of years that a forest may need to start to regenerate. For each subsequent year, $A(y,i)$ is calculated by increasing the age by 1 year for the area of forest that is not disturbed, returning the age to zero for a disturbed forest area, and entering age one for a previously disturbed forest area which, at that time, begins to regenerate. All area is treated equally in the model. With the calculated $A(y,i)$ and a normalized whole-plant NPP at age y ($F_{NPP}(y)$:

see more in section 3.4) the overall effect of disturbances on NPP is then given by

$$F_{pd}(i) = \int_0^{\infty} F_{NPP}(y) A(y,i) dy / \int_0^{\infty} F_{NPP}(y) A(y,0) dy. \quad (16)$$

From (12) and (14), we calculate the final NPP(i) in year i as follows:

$$NPP(i) = NPP_u(i) F_{pd}(i). \quad (17)$$

3. Parameter Estimation

While InTEC is constructed as a general terrestrial ecosystem C-budget model, our main application area at this stage is for Canada's forests. Therefore we will calibrate it using experimental data obtained from Canada's forest ecosystems. In order to apply InTEC to other terrestrial biomes, new calibrations may be required.

3.1. Abiotic Decomposition Factor

The Century and other models have used a Q_{10} -based equation to describe the relationship between soil temperature T_s and gross respiration rate R [Parton *et al.*, 1987]. Lloyd and Taylor [1994] found that the Q_{10} -based equation has two major problems. First, the value of Q_{10} is not constant, ranging from 1.3-3.3 as found in soil respiration studies

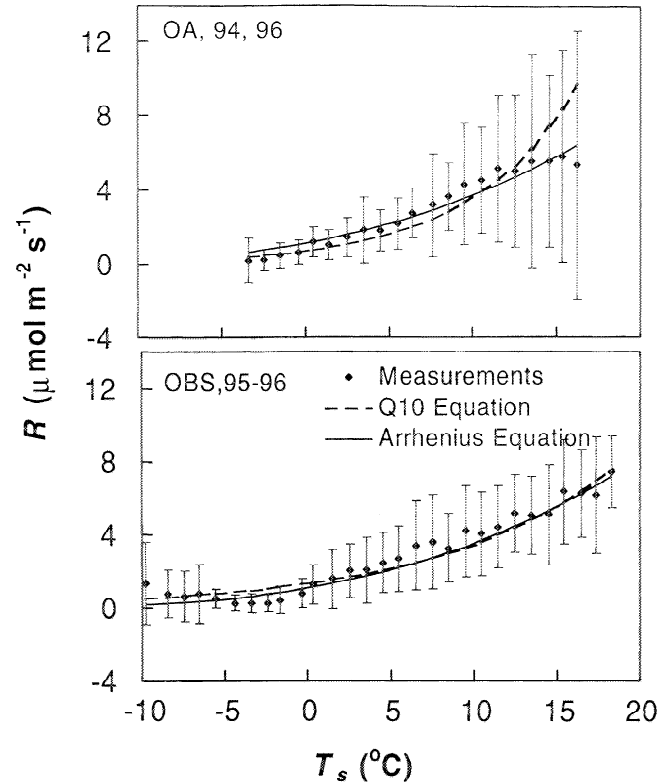


Figure 2. Comparison of respiration rates calculated using a modified Arrhenius equation [Lloyd and Taylor, 1994] and a Q_{10} -type equation with measurements made at the Boreal ecosystem-atmosphere Study (BOREAS) old black spruce (OBS) site in 1995 and 1996 and at the old aspen (OA) site in 1994 and 1996.

Table 2. Values of V_{m25} , J_{m25} , and f_p

	OBS	OBS	OA	OA	Mean
	1995	1996	1994	1996	($\pm\sigma$)
V_{m25}	14.6	16.1	25	29.9	15.4 (± 1.1)*
J_{m25}	41.7	46.1	71.44	85.40	43.9 (± 3.1)*
$f_{p,sun}$	7.3	6.8	7.3	6.6	7.0 (± 0.4)
$f_{p,shad}$	61.0	79.5	78.4	76.5	73.9 (± 8.7)

These values are obtained by fitting to measured photosynthesis rates at the BOREAS old black spruce (OBS) site in 1995 and 1996, and at the old aspen (OA) site in 1994 and 1996.

*For OBS only.

[Reich and Schlesinger, 1992]. Second, when a single Q_{10} value is used for a wide range of T_s , R is frequently overestimated at high T_s and underestimated at low T_s , thus introducing uncertainties in estimating the effect of climate change on C balance. To avoid these problems, we use a modified Arrhenius-type equation for the abiotic decomposition factor [Lloyd and Taylor, 1994]:

$$A = e^{-308.56 \left(\frac{1}{T_s(0)+46.02} - \frac{1}{T_s+46.02} \right)} \quad (18)$$

This equation yielded unbiased estimates of respiration rates over a wide range of T_s (from -5° to 40°C) in 15 ecosystems at different latitudes [Lloyd and Taylor, 1994]. The equation also matches R measurements better than a Q_{10} type best fit (Figure 2). The measurements were made at the Boreal Ecosystem-Atmosphere Study (BOREAS) Old Aspen (OA) site ($53^\circ 38' \text{N}$, $106^\circ 12' \text{W}$) in the Prince Albert National Park, Saskatchewan, and the Old Black Spruce (OBS) site ($55^\circ 53' \text{N}$ and $98^\circ 29' \text{W}$) near Thompson, Manitoba, during 1994–1996 [Goulden et al., 1998; W.J. Chen et al., 1999].

3.2. Photosynthesis Parameters

Values of f_p , V_{m25} and J_{m25} are given by fitting (4) to measured half hour canopy photosynthesis rates at the BOREAS OA site during 1994 and 1996 and at OBS site during 1995 and 1996 (Table 2). In the fitting process, we used the Wullschlegel's [1993] relationship between V_m and J_m at 25°C for boreal forest species, i.e., $V_{m25} = 0.35J_{m25}$.

The good agreement between simulated and measured canopy photosynthesis rates indicates that Farquhar's model and the canopy radiation model work well for boreal forests (Figure 3). For the OBS stand, V_{m25} values were 14.6 and $16.14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in 1995 and 1996, respectively, with corresponding V_m values of 6.58 and $8.39 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This result is consistent with the results of Dang et al. [2000] for the same OBS stand, who found that V_m ranged from 3.6 to $12.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, with a mean of $7.74 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. We use the mean values of OBS for Canada's forests because the majority of Canada's forests are conifer. The fraction dominated by p_{can1} and p_{can2} differs significantly between sunlit and shaded leaves but is similar for sunlit (or shaded) leaves of different species and in different years (Table 2). The overall average of leaf area index of Canada's forests is estimated to be 2.03 on the basis of satellite measurements using the same method of Liu et al. [1997]. On average, 63.1% of leaves are shaded and 36.9% are sunlit,

resulting in an overall f_p of 0.472. Table 3 lists the values of L_r and $\zeta\psi$ also based on these BOREAS measurements.

3.3. Growing Season Length

We assume that a growing season starts when all the following conditions are met: (1) 5-day running mean air temperature $T_a > 5^\circ\text{C}$, (2) no $T_a < 0^\circ\text{C}$ until the end of the year, and (3) heat units have accumulated to at least 40 degree-day with $T_a > 5^\circ\text{C}$. The value of heat units with $T_a > 5^\circ\text{C}$ is calculated by summing $[T_a(j) - 5]$ for j from 1 to k , where j is the day of the year, k is the day concerned, and if $T_a < 5^\circ\text{C}$, $T_a(j) - 5$ is treated as zero. The growing season ends when the following two conditions are met: (1) 5-day running mean $T_a < 5^\circ\text{C}$, and (2) for any given period afterward the heat unit in excess of 5°C is smaller than that below 5°C . Using these criteria, the growing season length is determined at Cameo, Prince Albert, Norway House, and Thompson, Canada, during the period from 1975 to 1996. The length is found to be highly correlated with mean spring (March–May) air temperature, with $r^2 = 0.64$ (Figure 4). The slope of the linear regression is 5.13 days per degree increase in the mean spring air temperature. Similar slope between measured leafing date and average April–May air temperature at the OA site for 4 years in 1994 and 1996–1998 are shown by Black et al. (2000). We thus determine the growing season length variation on the basis of mean spring air temperature.

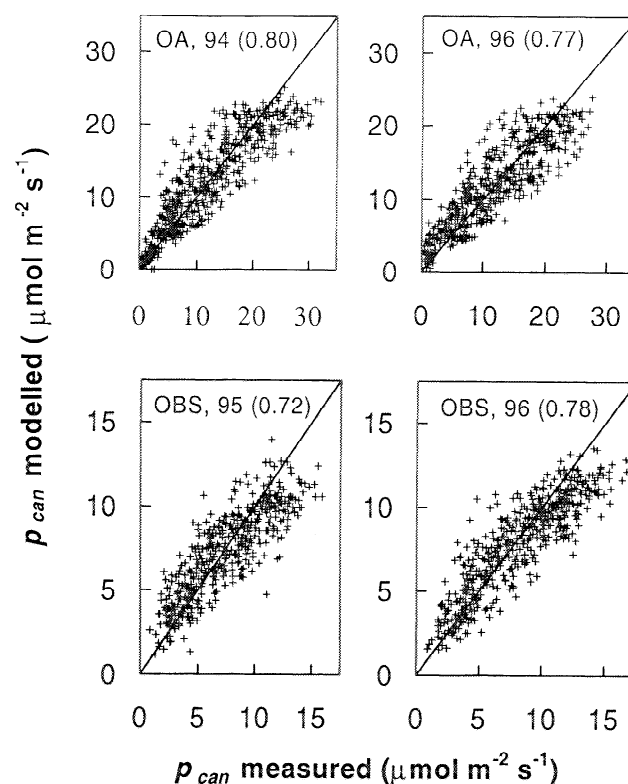


Figure 3. One-to-one comparison of canopy photosynthesis rate between simulations using the Farquhar's model and a canopy radiation model and measurements at the BOREAS old black spruce (OBS) site in 1995 and 1996 and at the old aspen (OA) site in 1994 and 1996. Values in parenthesis are r^2 .

Table 3. Mean Values for the Coefficients Representing the Effects of CO₂ Fertilization and Climate Warming (L_x), for the Correction Factors Accounting for the Effects of Diurnal and Seasonal Variations (ζ) on L_x , and for the Difference between L_x Values Calculated From Short Term (e.g., half-hour) Environmental Conditions and From Annual Means (ψ)

	OBS 1995	OBS 1996	OA 1994	OA 1996	Mean ($\pm\sigma$)
$\overline{L_1} \times 10^{-3}$	0.8	0.9	0.9	0.8	0.9(± 0.1)
$\zeta_{L_1, \rho} \psi_{L_1}$	1.16	1.16	1.15	1.13	1.15 (± 0.01)
$\overline{L_2} \times 10^{-3}$	1.9	2.0	2.0	1.9	2.0(± 0.1)
$\zeta_{L_2, \rho} \psi_{L_2}$	1.07	1.07	1.07	1.07	1.07 (± 0.00)
$\overline{L_{T_{1,1}}} \times 10^{-3}$	-15.9	-17.4	-17.0	-16.7	-16.8 (± 0.6)
$\zeta_{L_{T_{1,1}, \rho}} \psi_{L_{T_{1,1}}}$	1.15	1.15	1.12	1.12	1.14 (± 0.01)
$\overline{L_{T_{1,2}}} \times 10^{-3}$	-1.5	-1.6	-1.5	-1.8	-1.6 (± 0.1)
$\zeta_{L_{T_{1,2}, \rho}} \psi_{L_{T_{1,2}}}$	1.35	1.25	1.26	1.31	1.29 (± 0.05)
$\overline{L_{T_{1,3}}} \times 10^{-3}$	26.2	20.4	23.8	23.3	23.4 (± 2.4)
$\zeta_{L_{T_{1,3}, \rho}} \psi_{L_{T_{1,3}}}$	0.87	0.98	0.93	1.02	0.95 (± 0.06)
$\overline{L_{T_{2,1}}} \times 10^{-3}$	-5.8	-6.5	-6.3	-6.2	-6.2 (± 0.3)
$\zeta_{L_{T_{2,1}, \rho}} \psi_{L_{T_{2,1}}}$	1.23	1.22	1.18	1.17	1.20 (± 0.03)
$\overline{L_{T_{2,2}}} \times 10^{-3}$	-35.0	-35.9	-35.7	-35.4	-35.5 (± 0.4)
$\zeta_{L_{T_{2,2}, \rho}} \psi_{L_{T_{2,2}}}$	1.03	1.03	1.03	1.03	1.03 (± 0.1)
$\overline{L_{T_{2,3}}} \times 10^{-3}$	-3.2	-3.5	-3.5	-3.9	-3.5 (± 0.3)
$\zeta_{L_{T_{2,3}, \rho}} \psi_{L_{T_{2,3}}}$	1.08	1.04	1.14	1.08	1.08 (± 0.04)
$\overline{L_{T_{2,4}}} \times 10^{-3}$	87.1	86.8	86.9	86.9	86.9 (± 0.1)
$\zeta_{L_{T_{2,4}, \rho}} \psi_{L_{T_{2,4}}}$	0.97	0.97	0.98	0.98	0.98 (± 0.01)

The values are derived based on data measured at the BOREAS old black spruce (OBS) site in 1995 and 1996, and at the old aspen (OA) site in 1994 and 1996.

3.4. Relationship Between NPP and Age

Measurements of aboveground NPP for boreal needle-leaf evergreen trees showed that it changes substantially with age [Gower et al., 1996]. Assuming a constant proportion of NPP is allocated below ground, we modify Gower et al.'s relationship between aboveground NPP and stand age to obtain a normalized whole-plant NPP at age y , $F_{NPP}(y)$ (Figure 5). The value of $F_{NPP}(y)$ is assumed to increase linearly from age 0 to 22 years and to decrease to zero linearly at age > 138 years at the same rate during age 128-136 years. Since conifer forests are the dominant forests in Canada, we approximate the $F_{NPP}(y)$ for all Canada's forests with that in Figure 5.

4. Sensitivity Analysis

4.1. First Type of Uncertainties

Figure 6 shows the differences in C balance of Canada's forests caused by neglecting the effects of disturbance factors

and nondisturbance factors (see detailed data description by Chen et al., this issue). Neglecting the effects of disturbance factors would have overestimated C balance of Canada's forests in recent 2 decades (1980-1996) of ~56 Tg C yr⁻¹ by ~160%, or ~8% of the mean annual total NPP of ~ 1.1 Pg C yr⁻¹ [Chen et al., this issue]. For the same period the omission of nondisturbance factors would underestimate the C sink by ~200%, or ~10% of the mean annual total NPP.

For the nondisturbance factors, neglecting the effects of changes in climate, atmospheric CO₂ concentration, and N deposition would have underestimated the C balance of Canada's forests by ~60%, ~40%, and ~100% during 1980-1996, respectively (Figure 7). Relative to the mean annual total NPP during 1980-1996, the underestimation would have been ~3%, ~2%, and ~5%, respectively. Neglecting the secondary effects of climate change, namely, the increases in growing season length and net N mineralization and N fixation rates, would have underestimated C sink by ~38% and ~43%, respectively. The omission of the direct effect of climate change on NPP and soil decomposition would have caused an overestimation of the C balance of Canada's forests during 1980-1996 by ~27%, or ~1% the mean annual total NPP.

4.2. Second Type of Uncertainties

The error in the mean national NPP value is estimated to be within $\pm 25\%$ [Liu et al., 1997]. A 25% error in NPP may result in ~500% uncertainty in the C balance of Canada's forests during 1980-1996 if NPP, R_h , and ξA_f in that year are estimated independently, even if R_h and ξA_f are estimated without error. In reality, the accuracy of R_h and ξA_f is much lower than that of NPP, and thus the uncertainty could be > 1000%.

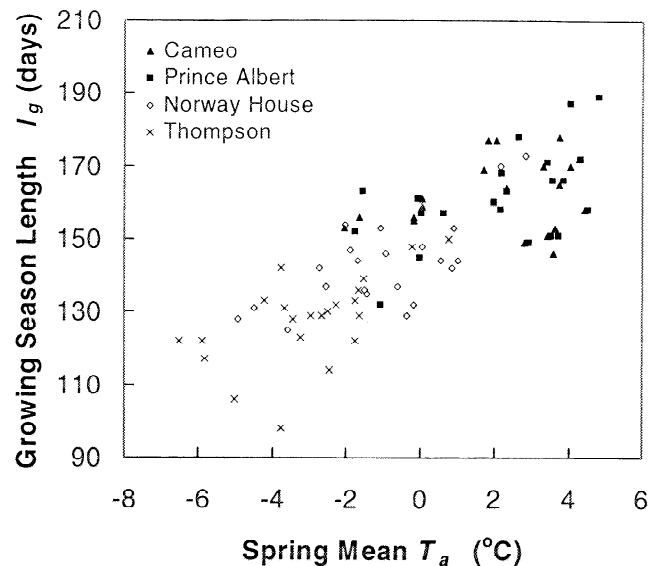


Figure 4. The relationship between mean spring air temperature (March-May) and growing season length at Cameo (53°17'N, 106°33'W), Prince Albert (53°13'N, 105°40'W), Norway House (53°59'N, 97°50'W), and Thompson (55°48'N and 97°52'W). The growing season is defined in text.

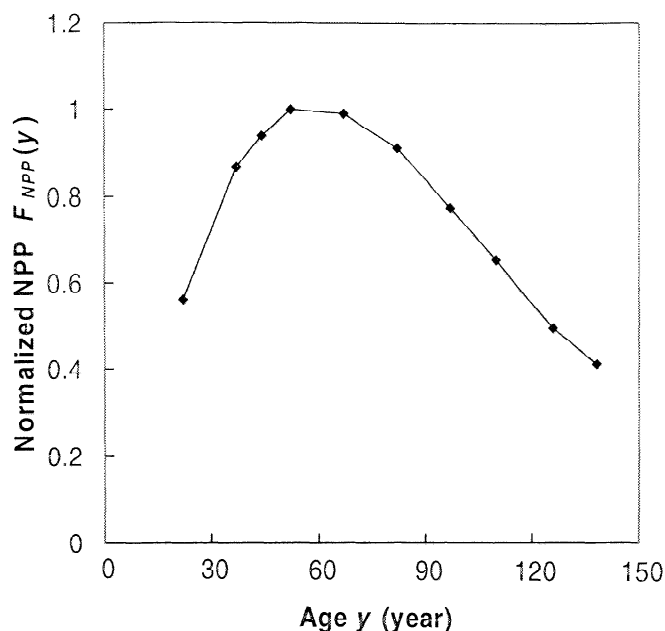


Figure 5. The relationship between NPP normalized by its maximum and stand age for boreal needle-leaf evergreen trees.

The introduction of the historical change approach can reduce the uncertainty substantially. To simplify, we first consider the effects of nondisturbance factors (i.e., assume a constant disturbance rate). Inserting (12) into (2) gives

$$\frac{dC(i)}{di} = \text{NPP}(i) \left\{ 1 - K(i) e^{-\sum_{m=1}^i \kappa(m)} \left[\frac{1}{\prod_{k=1}^i \frac{2 + \chi(k)}{2 - \chi(k)}} \right] + \sum_{j=0}^i \left(e^{\sum_{m=1}^j \kappa(m)} / \prod_{k=j+1}^i \frac{2 + \chi(k)}{2 - \chi(k)} \right) \right\} \quad (19)$$

Equation (19) indicates that a 25% error in NPP will result in

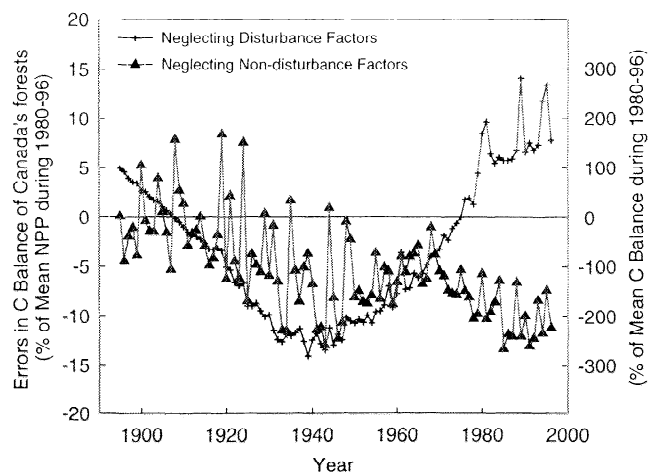


Figure 6. Errors in C balance of Canada's forests, caused by neglecting the effects of disturbance factors (including forest fire, insect-induced mortality, and clear-cut harvest) and nondisturbance factors (including climate, CO₂, and N deposition), as percentages of mean annual total NPP or C balance during 1980-1996.

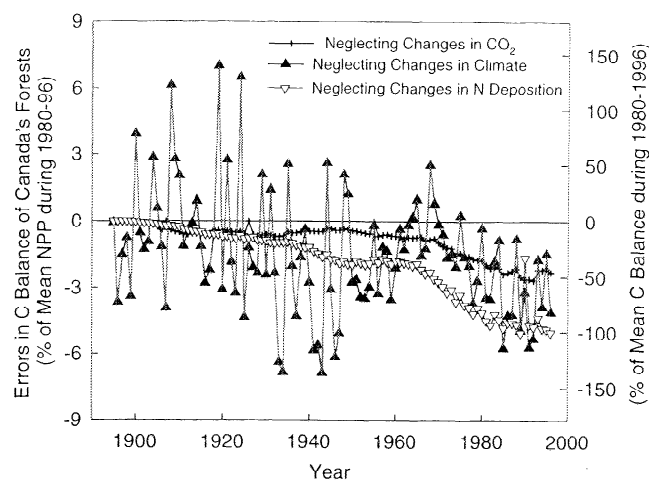


Figure 7. Errors in C balance of Canada's forests, caused by neglecting the effects of changes in climate, atmospheric CO₂ concentration, and N deposition, as percentages of mean annual total NPP or C balance during 1980-1996.

only 25% error in the C balance. The error appears to be even smaller during 1980-1996 if disturbance factors are considered together (Figure 8). This is because during the low-disturbance period from 1930-1970 a larger amount of C would have been accumulated if the NPP were 125% of the actual NPP than if the NPP were 75% of the actual NPP. This larger amount of C accumulation led to a higher soil decomposition rate in recent decades, causing the C balance with the 125% of the actual NPP being only slightly larger than those with the 75% of the actual NPP and the actual NPP.

While the above analysis shows that the historical change approach can reduce uncertainty in C balance substantially, its requirement for historical data also causes additional errors. Measurement errors in temperature and precipitation, N deposition, atmospheric CO₂ concentration, and disturbance rate may cause uncertainties in C balance estimation. For the C balance of Canada's forests during 1980-1996 [Chen *et al.*, this issue], a 10% error each in climate, N deposition, or atmospheric CO₂ concentration would cause ~3%, 6%, or ~1% Tg C yr⁻¹ error in C balance, respectively. The C emission due to fire is controlled by area burned, carbon density of the burned area, and fraction of carbon consumed during fires [French *et al.*, 1999]. The data of area burned in North American boreal forests is accurate to within 5% since late 1970s [French *et al.*, 1999], but is less accurate before then. Using spatially explicit data of C density and data of fraction of carbon consumed during controlled fires in Canada and field observation in Alaska for the period from 1980 to 1994, French *et al.* [1999] estimated that the ratio of 1σ of ξ to its average value is 37%. The use of a constant value in this study thus may subject to an uncertainty ~37% in ξ if we use the 1σ value, with a combined error in ξA_f being ~50%. Using this error of 50% in ξA_f, we estimate ~15% error in C balance for the Canada's forests during 1980-1996. Note that the magnitude of these errors may fluctuate from year to year.

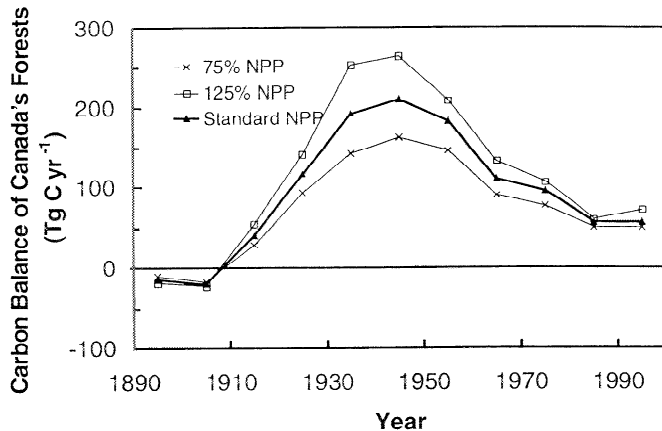


Figure 8. Errors in C balance of Canada's forests as a result of different annual NPP estimates in the calibration year, 1994, while all other inputs remained the same. The 10-year average is shown here, with the first point for 1895-1899 and the last point for 1990-1996.

Overall, if we can estimate temperature and precipitation, N deposition, and atmospheric CO₂ concentration to within 10% each, fire emission to within 50%, and NPP in calibration year to within 25%, we may expect that the error be <50% of the C balance of Canada's forests during 1980-1996, or within 25 Tg C yr⁻¹. Since many of these errors may actually cancel mutually, the real accuracy of C balance should be better than the sum of individual errors.

4.3. Other Uncertainties

There are issues that are not considered in this study but may cause additional uncertainties in the C balance. The key issues include (1) spatial and temporal variations in climate and N deposition, (2) effects of thaw depth and water table on soil respiration rates, and (3) variability in successional stand dynamics for different species under variable environmental conditions.

Recent studies have shown that consideration of spatial and temporal variations in climate and N deposition is potentially important in C sink estimation [Rastetter *et al.*, 1992; Tian *et al.*, 1998, 1999]. Canada represents a region with different local climate trends over the last 100 years: Continental interiors warmed more than the coastal margins and even cooling in the Northeast [Environment Canada, 1995]. The N deposition rate over Canada was also spatially variable [Ro *et al.*, 1995]. Spatially explicit analysis can help address this issue and facilitate testing model results against site measurements, such as those at the BOREAS OA and OBS sites. To conduct such spatially explicit analysis, historical data of climate, N deposition, and disturbances at high spatial resolution are needed. The climate data are generally available. In Canada, high spatial resolution data of N deposition and disturbance rates are available in recent years but not over the historical period. Since the C balance is affected substantially by the historical conditions of N deposition and disturbance rates, we emphasize the need for these data.

If warming leads to an increase in thaw depth in frozen soil or a change in drainage in areas with high water table, C balance could substantially shift, with increased release of C stored over past millennia. On the other hand, the associated increase in net N mineralization rate could increase C uptake by plants since high-latitude plants are highly N limited. To quantify these two opposite effects on C balance, high quality, high spatial, and temporal information of thaw depth and water table are needed.

Successional stand dynamics and the associated biogeochemistry could influence the C cycle [Zimov *et al.*, 1999]. In this study, we use an empirical NPP-age relationship to represent the postdisturbance vegetation dynamics. We emphasize, however, the need to consider successional dynamics for different species under different environmental conditions, such as climate, soil, topography, etc.

5. Summary and Concluding Remarks

Two uncertainties frequently exist in estimates by regional forest C budget models, owing to exclusion of certain factors in the C balance estimation and to the fact that the C balance is a small difference between several large fluxes. In this study we propose new modeling approaches to reduce these uncertainties by considering all major factors and their historical changes. The historical change approach assumes that the C and N exchanges between terrestrial ecosystems and atmosphere were in equilibrium under the mean climate conditions, mean N deposition rate, and mean disturbance rates during the preindustrial period. In any year since then the C balance is estimated as the sum of changes in all these fluxes relative to their respective preindustrial values.

These new modeling approaches were implemented using an integrated terrestrial ecosystem C-budget model (InTEC). The core of InTEC is a mechanistic integration of the Century model for coupled ecosystem C-N cycles with Farquhar's biochemical model of leaf photosynthesis. The integration is achieved through new spatial and temporal scaling algorithms. First, we used a canopy radiation model with sunlit-shaded leaf separation to integrate leaf photosynthesis to stand level. Second, we derived statistical relationships between interannual changes in NPP and the averages of climatic variables, atmospheric CO₂ concentration, and N deposition. A covariance method was used to account for the effects of diurnal and seasonal variability of major climate factors and NPP on the above relationships. In this way, detailed temporal and spatial integration of NPP is needed for only one recent calibration year, and NPP for all others years can be determined using the above relationships.

Parameters of the InTEC model were calibrated using data derived from Canada's forest ecosystems such as the BOREAS data at the OBS (1995 and 1996) and OA (1994 and 1996) sites. Specifically, we calibrated the abiotic factor for soil respiration, and photosynthetic parameters and growing season length for NPP. A relationship between NPP and age was adopted from Gower *et al.* [1996].

Our sensitivity analysis suggested each of the two types of uncertainties may result in 200-1000% errors in the C balance of Canada's forests during recent decades (1980-1996). By

implementing these new approaches in InTEC the overall uncertainty can be reduced to within 50% if climate and atmospheric chemistry are accurate to within 10% each, C release due to forest fire is accurate to within 50%, and NPP in the calibration year is accurate within 25%. There are issues that are not considered in this study but may cause additional uncertainties in the C balance. They may include (1) spatial and temporal variations in climate and N deposition, (2) effects of thaw depth and water table on soil respiration rates, and (3) variability in successional biogeochemistry under different environmental conditions.

Appendix: Formula for L_x

$$L_1 = \frac{15\alpha\Gamma}{(\alpha c_a - \Gamma)(4.5\alpha c_a + 10.5\Gamma)} \quad (\text{A1})$$

$$L_{T1,1} = -0.056c_a L_1 \quad (\text{A2})$$

$$L_{T1,2} = L_{T2,3} = -L_1 c_a \frac{198.2h_r}{(240.97 + T_a)^2} e^{\frac{17.502T_r}{240.97+T_r}} \quad (\text{A3})$$

$$L_{T1,3} = \left\{ \frac{\text{LAI}_{\text{sun}} J_m}{\text{LAI}_i J} [0.714 - \frac{0.714J_m - 0.1086S_{\text{sun}}}{\sqrt{(J_m + 0.38S_{\text{sun}})^2 - 1.064J_m S_{\text{sun}}}}] + \frac{\text{LAI}_{\text{shad}} J_m}{\text{LAI}_i J} [0.714 - \frac{0.714J_m - 0.1086S_{\text{shad}}}{\sqrt{(J_m + 0.38S_{\text{shad}})^2 - 1.064J_m S_{\text{shad}}}}] \right\} \cdot \left[0.0531 - \frac{26461.9}{(T_a + 273)^2 (1 + e^{\frac{3147.7 - 85.4T_r}{T_r + 273}})} \right] \quad (\text{A4})$$

$$L_{N1} = \frac{J_m \text{LAI}_{\text{sun}}}{JN_i \text{LAI}_i} [0.714 - \frac{0.714J_m - 0.1086S_{\text{sun}}}{\sqrt{(J_m + 0.38S_{\text{sun}})^2 - 1.064J_m S_{\text{sun}}}}] + \frac{J_m \text{LAI}_{\text{shad}}}{JN_i \text{LAI}_i} [0.714 - \frac{0.714J_m - 0.1086S_{\text{shad}}}{\sqrt{(J_m + 0.38S_{\text{shad}})^2 - 1.064J_m S_{\text{shad}}}}] \quad (\text{A5})$$

$$L_2 = \frac{\alpha(k_{co} + \Gamma)}{(\alpha c_a - \Gamma)(\alpha c_a + k_{co})} \quad (\text{A6})$$

$$L_{T2,1} = -\frac{0.056\Gamma(\alpha c_a + k_{co})}{\alpha(k_{co} + \Gamma)} L_2 \quad (\text{A7})$$

$$L_{T2,2} = -\frac{(0.074k_{co} - 0.291\Gamma)(\alpha c_a - \Gamma)}{\alpha(k_{co} + \Gamma)} L_2 \quad (\text{A8})$$

$$L_{T2,4} = 0.0875 - \frac{26461.9}{(T_a + 273)^2 (1 + e^{\frac{3147.7 - 85.4T_r}{T_r + 273}})} \quad (\text{A9})$$

$$L_{N2} = 1/N_i \quad (\text{A10})$$

Notation

A_d, A_f, A_t	disturbed, burned, and total forest area, m^2
c_i, c_a	Intercellular and atmospheric CO_2 concentration, $\mu\text{mol mol}^{-1}$
C_x	C content in pool x (subscript), g C m^{-2}
$F_{NPP}(y)$	normalized NPP as a function of age y
F_p	fraction of p_{can} determined by p_{can1}
F_{pd}	coefficient for the effect of disturbance on NPP
F_x	C allocation coefficient from NPP to pool x
H_r	air relative humidity, %
J, J_m	electron transport rate and maximum J , $\mu\text{mol electron m}^{-2} \text{s}^{-1}$
$J_{\text{sun}}, J_{\text{shad}}$	electron transport rate on sunlit and shaded leaves, $\mu\text{mol electron m}^{-2} \text{s}^{-1}$
k_{co}	coefficient associated with enzyme kinetics, $\mu\text{mol mol}^{-1}$
$K_{x,y}$	C transfer coefficient from pool x to y , yr^{-1}
L_x	Coefficients for the effects of nondisturbance factors on photosynthesis (see detail formula in Appendix)
LAI_i	total leaf area index, $\text{m}^2 \text{m}^{-2}$
LAI_{sun}	sunlit leaf area index, $\text{m}^2 \text{m}^{-2}$
LAI_{shad}	shaded leaf area index, $\text{m}^2 \text{m}^{-2}$
L_g	growing season length, day
N_i, N_{max}	actual and optimal leaf N content per unit leaf area, g N m^{-2}
NPP, NPP_u	net primary productivity, and NPP based on non-disturbance factors, $\text{g C m}^{-2} \text{yr}^{-1}$
$P(i)$	mean annual gross photosynthesis rate, $\text{g C m}^{-2} \text{yr}^{-1}$
p_1, p_2	Instantaneous leaf gross photosynthesis rate limited by electron transport and by rubisco activity, $\text{g C m}^{-2} \text{s}^{-1}$
$P_{\text{can1}}, P_{\text{can2}}$	Instantaneous canopy gross photosynthesis rate limited by electron transport and by rubisco activity, $\text{g C m}^{-2} \text{s}^{-1}$
Q	occurrence frequency of fire and insect-induced mortality, yr^{-1}
R, R_h	gross and heterotrophic respiration rate, $\text{g C m}^{-2} \text{s}^{-1}$
T_s, T_a	soil and air temperature, $^{\circ}\text{C}$
V_m	maximum carboxylation rate, $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$
VPD	air water vapour deficit, kPa
$\zeta_{L, p_{\text{can}}}$	scaling factor accounting for the effects of temporal and spatial variations in L_x and P_{can} on dP_{can}
ψ_{L_x}	ratio of assemble average of L_x to L_x calculated using annual mean environmental conditions
A	abiotic decomposition factor
Γ	CO_2 compensation point without dark respiration, $\mu\text{mol mol}^{-1}$
α	ratio of c_i to c_a
χ	relative change rate of $P(i)$ as a function of changes in non-disturbance factors
ξ_x	C loss from pool x due to forest fire, $\text{g C m}^{-2} \text{yr}^{-1}$
σ	Standard deviation
A	subscript for atmosphere
Subscripts	
Cr, fr, l, w	coarse root, , fine root, leaf, wood
Cd, fd	coarse structural detritus, fine structural detritus
m, md, p, s	microbe, metabolic detritus, passive soil, slow soil
Fu, lo, pa	fuel wood, longterm storage wood products, paper and pulp products

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