An integrated terrestrial ecosystem carbon-budget model based on changes in disturbance, climate, and atmospheric chemistry

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Abstract

Disturbances (e.g. fire, insect-induced mortality, and harvest) and management practices (e.g. planting) affect the forest carbon (C) cycle, so do non-disturbance climatic and atmospheric factors (e.g. growing season length and temperature, abiotic decomposition factor, annual precipitation, atmospheric CO_2 concentration, and nitrogen (N) deposition). Previous studies investigated the effects of these factors individually or in some combinations, but not their integrated effects at regional and global scales. This study describes an Integrated Terrestrial Ecosystem C-budget model (InTEC), which integrates effects of all these factors on the annual C cycle of a forest region. InTEC is based on the Farquhar's leaf photosynthesis model, the Century C cycle model, the net N mineralization model of Townsend et al. [Ecol. Appl., 6 (1996) 806] and an age–NPP relationship derived from forestry inventory-based age–biomass relationships. To integrate these existing models, which were developed for different purposes and had different spatial and temporal scales, into a coherent mechanistic model, we (1) develop a spatial and temporal up-scaling algorithm to use the instantaneous leaf-level model for a region at annual time step; and then (2) combine the upscaled results with an age–NPP relationship to obtain the annual NPP of a forest region. A historical change approach is then used to describe the regional annual C cycle, which not only improves the accuracy of its historical and present estimates, but also enables us to predict its future responses, both of which are critical in formulating mitigation and adaptation strategies for global changes. Applying InTEC to Canada's forests, we first investigate the impacts of each factor on the C cycle over the short term (i.e. in the year of perturbation) and the long term (i.e. in the years after perturbation). The short-term and long-term effects are determined by changing one of the 10 factors in year 1 since the industrialization while keeping this factor in all other years and all other factors in all years at pre-industrial levels. Integrating all these short-term and long-term effects for the actual historical data of the 10 external forcing factors, we then estimate that the annual mean NBP (= NPP — soil respiration — fire emission — forest praoducts oxidation) of Canada's forests was 40 ± 20 Tg C per year (i.e. a sink) in 1810s, reduced to -131 ± 66 Tg C per year (i.e. a source) in 1870s, increased thereafter to a maximum of 200 ± 100 Tg C per year in 1930s, and decreased again to 57 ± 27 Tg C per year in 1990s. From 1800 to 1998, the aboveground biomass of Canada's forests increased by $\sim 19\%$, while the soil C stock increased by $\sim 2\%$. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Canada; Forest; C balance; Model; Disturbance; Climate; Atmospheric chemistry

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1. Introduction

Global land use changes (LUC) was estimated to release 1.6 ± 1.0 Pg per year (1 Pg = 10^{15} g) carbon (C) to the atmosphere during 1980s (Houghton et al., 1996). This estimate, along with that of fossil fuel emissions, accumulation in the atmosphere, and ocean sink, suggested that during 1980s a missing sink of 1.8 ± 1.6 Pg C per year existed in the terrestrial biomes that were not subject to LUC (Houghton et al., 1996).

In searching for the missing sink, the effects of disturbances (e.g. fire, insect-induced mortality, and harvest), climatic variations (e.g. growing season length l_g, growing season temperature $T_{a,g}$, annual precipitation APPT, abiotic decomposition factor Λ), and changes in atmospheric chemistry (atmospheric CO_2 concentration and nitrogen (N) deposition) were each investigated (e.g. Bazzaz, 1990; Kurz et al., 1992; Dai and Fung, 1993; Kolchugina and Vinson, 1993; Turner et al., 1995; Townsend et al., 1996; Kurz and Apps, 1999). For example, the 1995 IPCC report estimated that the Northern hemisphere forest regrowth as a result of changes in age class distribution, caused by variations in disturbance rates, increased terrestrial C sink by 0.5 ± 0.5 Pg C per year during the 1980s (Houghton et al., 1996). In the same IPCC report, N deposition was suggested to increase global terrestrial C sink by 0.2–1.0 Pg C per year, CO_2 fertilization by 0.5–2.0 Pg C per year, and climatic changes by 0–1.0 Pg C per year during the 1980s. Other studies have investigated the effects of some combinations of these factors. For example, Melillo et al. (1993) and Post et al. (1997) integrated the effects of changes in CO_2, climate, and N deposition. Aber and Driscoll (1997) investigated land use, climatic variation, and N deposition on C storage for six northern hardwood forest sites. However, no existing model has attempted to integrate the effects of all these disturbance and non-disturbance factors on the C cycle of a forest region. Due to the complex interactions and feedback among these effects, accurate regional and global terrestrial ecosystem C balance cannot be obtained by simply summing the estimates for individual factors. Therefore, a comprehensive analysis, which mechanistically integrates all of these disturbance and non-disturbance factors, is needed (Fung, 1996; Schimel et al., 1997; Potter, 2000).

This paper describes an Integrated Terrestrial Ecosystem C-budget model (InTEC), which integrates the effects of all these factors on the forest carbon cycle. Realizing that InTEC is a complex model, which involves a large number of variables and processes at different spatial and temporal scales, we first provide a brief road map in Section 2 by outlining the model strategy. Detailed model description is then given in Section 3. The model has been applied to Canada's 417.6 Mha forests (Canadian Forest Service, 1993), with application results being reported in Section 4.

2. Model strategy

The C balance of a forest region is the sum of changes in all biomass, soil, and product C pools (Fig. 1). The C in soil and product pools come from biomass pools, which in turn are resulted from NPP. NPP changes with climate, atmospheric conditions, and stand age which in turn is a result of disturbances. Therefore, the C balance of a forest region is a function of these external forcing factors. In this study, we use the response function of NPP to changes in disturbance rates in year i, $\phi_{\mathrm{NPP}d}(i)$, and the response function of NPP to climatic and atmospheric changes in year i, $\phi_{\mathrm{NPP}n}(i)$, to describe the effects of the corresponding factors. The value of $\phi_{\mathrm{NPP}d}(i)$ is determined only by the changes in disturbance rates while keeping the climatic and atmospheric variables at their mean pre-industrial levels, while that of $\phi_{\mathrm{NPP}n}(i)$ is determined only by the climatic and atmospheric changes while keeping disturbances at their mean pre-industrial rates. Therefore, under the mean pre-industrial disturbance rates and climatic and atmospheric conditions, $\phi_{\mathrm{NPP}d}(0)$ and $\phi_{\mathrm{NPP}n}(0)$ equal 1, and NPP(0) was a constant. For any year since the industrialization, NPP was given by

$$\mathrm{NPP}(i) = \phi_{\mathrm{NPP}d}(i)\,\phi_{\mathrm{NPP}n}(i)\,\mathrm{NPP}(0). \tag{1}$$

The details of how to determine $\phi_{\mathrm{NPP}d}(i)$ from relationships between age class composition and

disturbance rates and an age–NPP relationship are given in Section 3.1. The Farquhar's leaf photosynthesis model is used for describing the effects of climatic and atmospheric changes on NPP in Section 3.2 (Farquhar et al., 1980; Bonan, 1995). To upscale the leaf photosynthesis to a region at an annual time step at which C and N cycles are investigated in this study, a spatial and temporal scaling algorithm is developed. Because leaf N content is a very important variable affecting $\phi_{\mathrm{NPP}n}(i)$, and involves the entire N cycle in forest ecosystems, a separate section (i.e. Section 3.3) is devoted to it. With known values of $\phi_{\mathrm{NPP}d}(i)$ and $\phi_{\mathrm{NPP}n}(i)$, the value of NPP(0) can be determined if NPP in a calibration year is known. In the case of Canada's forests, we choose 1994 as the calibration year, and NPP in this year is used as a base to calculate NPP(0) retrospectively.

Fig. 2 shows a more detailed structure of In-TEC. As Fig. 2 shows, disturbances also affect C transfer from biomass to soil and product pools. For example, fires release a fraction of biomass and soil C into the atmosphere, and transfer the remaining biomass C into soil pools. Harvest transfers a fraction of biomass into forest product C pools, and the remaining to soil C pools, while insect-induced mortality transfers all biomass to soil C pools. We describe the C cycle in Section 3.4, patterned to the widely tested Century model (Parton, et al., 1987; Schimel et al., 1996), except for the following four modifications. (1) NPP is determined every year since the industrialization using procedures discussed above; (2) Instead of using a constant Q_{10} to calculate Λ, we use a modified Arrhenius-type equation of Lloyd and Taylor (1994); (3) Disturbance effects on inter-pool C transfer are considered in the C cycle; (4) The soil structural C pool is divided into coarse and fine components to better characterize forest detritus of different residence times.

3. Model description

3.1. The response function of NPP to disturbances ϕ_{NPPd}

The stand age distribution $A(y, i)$ can be determined using a Weibull distribution:

$$A(y, i) = \frac{A_t q(i)\,\mathrm{e}^{-(q(i)y)^s}}{\varphi(1/s + 1)},\tag{2}$$

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). We further assume that only mature forests are harvested. At $y = 0$ (i.e. for areas disturbed and yet to regenerate), $A(0, i)$ was the difference between the disturbed and planted areas in previous n years, where n is the average age that a forest may need to start to regenerate. For example, $n = 5$ for Canada's forests, with a range of 1–10 years (Bunce, 1989). For each subsequent year, $A(y, i)$ is calculated by increasing the age by one year for not disturbed forest areas, returning the age to zero for newly disturbed forest areas, and entering age one for previously disturbed forest areas which at that time begin to regenerate. In this study, all areas are treated equally, and no spatial detail is involved. With the calculated $A(y, i)$ and $F_{\mathrm{NPP}}(y)$, the overall effect of disturbances on NPP is then given by
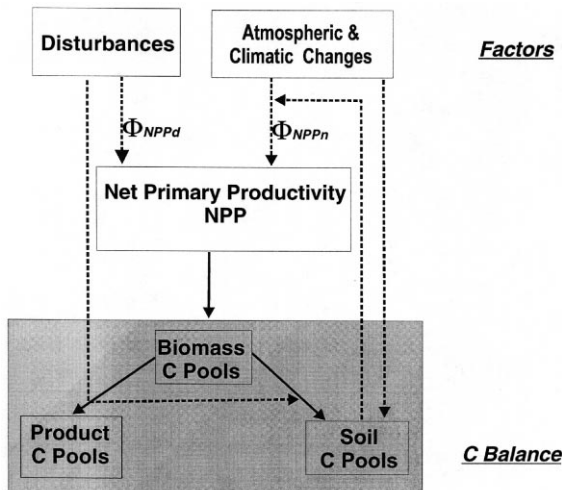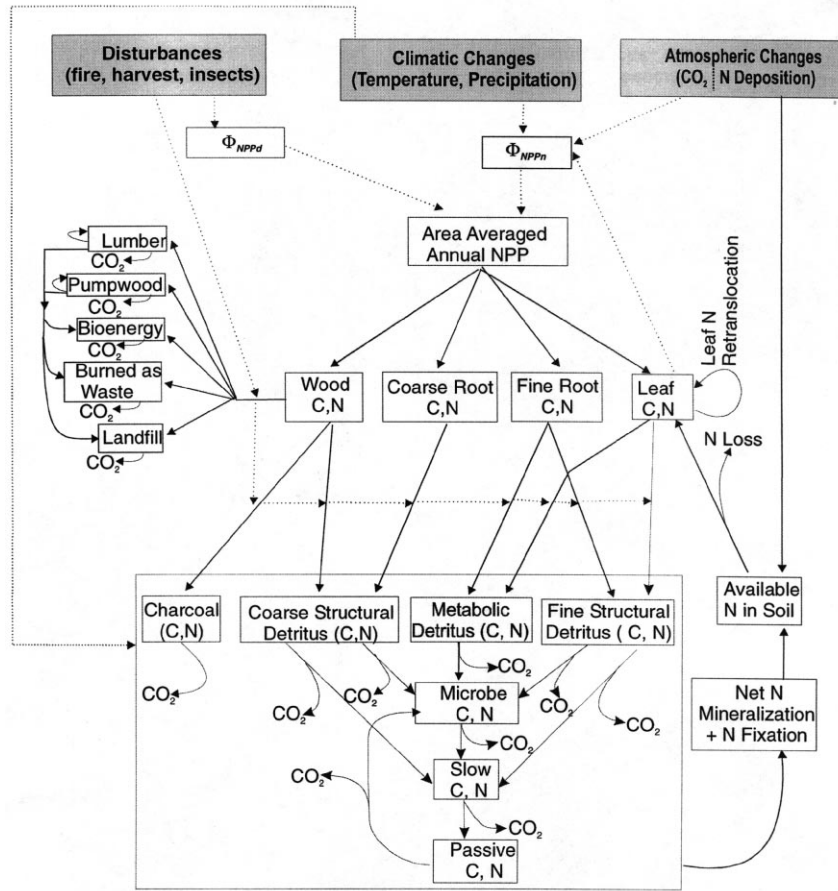

Fig. 1. Concept chart of an Integrated Terrestrial Ecosystem C-budget model (InTEC) for estimating the effects of changes in disturbance rates, climate, and atmospheric chemistry. Dished arrows indicate influences, and solid arrows show C–N flows.

Fig. 2. Same as Fig. 1 except with a more detailed structure.

$$\phi_{\text{NPP}d}(i) = \int_0^\infty F_{\text{NPP}}(y)A(y,i)\,dy \Big/ \int_0^\infty F_{\text{NPP}}(y)$$
$$A(y,0)\,dy. \tag{3}$$

3.2. The response function of NPP to non-disturbances ϕ_{NPPn}

For C_3 plants, which include all Canada's forests species, the instantaneous photosynthesis rate of a single leaf p is limited by the minimum of the two values (Farquhar et al., 1980; Bonan,

1995; Luo et al., 1996):

$$\begin{cases} p_1 = J\dfrac{c_i - \Gamma}{4.5c_i + 10.5\Gamma}, \\[2mm] p_2 = V_m\dfrac{c_i - \Gamma}{c_i + k_{\text{co}}} \end{cases} \tag{4}$$

where p_1 and p_2 are leaf gross photosynthesis limited by electron transport and rubisco activity, respectively. The values of J, V_m, c_i, Γ, and k_{co} in Eq. (4) are given by (Sellers et al., 1992; Bonan, 1995):

$$\begin{cases} J=[J_m+0.38S-\sqrt{(J_m+0.38S)^2-1.064J_mS}]/1.4 \\ V_m=V_{m25}\dfrac{N_l}{N_{l\max}}a_{Vm}^{\frac{T_a-25}{10}}/[1+e^{\frac{85.4T_a-3147.7}{T_a+273}}] \\ \Gamma=40.2\times1.75^{\frac{T_a-25}{10}} \\ k_{co}=300\times2.1^{\frac{T_a-25}{10}}+209\times1.75^{\frac{T_a-25}{10}} \\ c_i=\alpha c_a \end{cases}, \tag{5}$$

where $J_m=[J_{m25}(N_l/N_{l\max})a_{jm}^{(Ta-25)/10}]/[1+\exp((85.4T_a-3147.7)/(T_a+273))]$. The meanings of other terms are listed in Notation. Eq. (5) shows that p is affected by climatic variables (i.e. T_a, S, and h_r) and atmospheric variables (i.e. c_a and N deposition). The effect of N deposition on p is incorporated through $N_l/N_{l\max}$ (see details in Section 3.3).

The area-averaged annual gross photosynthesis rate of a forest region in year i, $P(i)$, is then given by integrating p for all leaves (x) over the whole forest region (y) and time periods during the year (t)

$$P(i)=\frac{1}{A_t}\int_t\int_y\int_x p\,\mathrm{d}x\,\mathrm{d}y\,\mathrm{d}t, \tag{6}$$

There are many ways to carry out this integration for all leaves in a stand (Norman, 1993). One way, simple yet effective, is to stratify a canopy into sunlit and shaded leaves (Norman, 1993), since T_a, c_a, and h_r are more or less the same for all leaves in a canopy because canopy air is often well mixed during daytime. This stratification is essential because irradiation changes greatly for different leaves depending on their positions relative to the sun, resulting in different J values for different leaves in the canopy. With this stratification and canopy radiation models (Black et al., 1991; Chen et al., 1999a), we calculate the instantaneous canopy photosynthesis rate, p_{can}, by the minimum of

$$\begin{cases} p_{can1}=(J_{sun}L_{sun}+J_{shad}L_{shad})\dfrac{c_i-\Gamma}{4.5c_i+10.5\Gamma}, \\ p_{can2}=V_m\dfrac{c_i-\Gamma}{c_i+k_{co}}L_t, \end{cases} \tag{7}$$

where L_{sun} is the sunlit leaf area index, given by $LAI_{sun}=2(1-P(\theta))\cos\theta$, where $P(\theta)$ is the gap fraction at the view zenith angle θ, calculated as $P(\theta)=e^{-G(\theta)\Omega LAI_t/\cos\theta}$ (Nilson, 1971; Chen et al., 1997). The shaded leaf area index, L_{shad}, thus equals the difference of total leaf area index L_t and L_{sun}. Assuming no significant changes in morphology of leaves occurred since the industrialization, we can calculate the change in area-averaged L_t in year i by

$$\mathrm{d}L_t(i)/L_t(i)=\mathrm{d}C_l(i)/C_l(i). \tag{8}$$

The values of J for sunlit leaves and shaded leaves, J_{sun} and J_{shad}, are calculated by replacing S in Eq. (5) with S_{sun} and S_{shad} respectively, where S_{sun} and S_{shad} are calculated following Black et al. (1991) and Chen et al. (1999a).

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

$$p_{can}=f_p p_{can1}+(1-f_p)p_{can2}. \tag{9}$$

With p_{can}, we reduce Eq. (6) to

$$P(i)=\frac{1}{A_t}\int_t\int_y p_{can}(y,t)\,\mathrm{d}x\,\mathrm{d}t. \tag{10}$$

While it is theoretically possible to calculate $P(i)$ for each year since the industrialization, such an operation is practically limited by data availability. 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 $P(i)$, $(\mathrm{d}P(i)/[P(i)\mathrm{d}i])$, and the external forcing factors. Differentiating Eq. (10) gives

$$\frac{\mathrm{d}P(i)}{\mathrm{d}i}=\underbrace{\int_t\int_y\frac{\mathrm{d}p_{can}(y,t)}{A_t}\mathrm{d}y\,\mathrm{d}t}_{(I)}+\underbrace{\int_t\frac{p_{can}(y,t)}{A_t}\frac{\partial y}{\partial i}\mathrm{d}t}_{(II)}$$
$$+\underbrace{\int_y\frac{p_{can}(y,t)}{A_t}\frac{\partial t}{\partial i}\mathrm{d}y}_{(III)}, \tag{11}$$

where term I represents the effect on $dP(i)/di$ caused by changes in $p_{can}(y, t)$, while term II and III represent, respectively, the effects caused by changes in forest cover area and growing season length (l_g). The value of $dp_{can}(y, t)$ is given by differentiating Eq. (9):

$$dp_{can}(y, t)$$
$$= f_p p_{can}[L_1 dc_a + (L_{T1,1} + L_{T1,2} + L_{T1,3})dT_a$$
$$+ L_{N1}dN_l + L_{L1,1}dL_{sun} + L_{L1,2}dL_{shad}]$$
$$+ (1 - f_p)$$
$$p_{can}[L_2 dc_a + (L_{T2,1} + L_{T2,2} + L_{T2,3} + L_{T2,4})dT_a$$
$$+ L_{N2}dN_l + L_{L2}dL_t], \tag{12}$$

where L_1, L_2, $L_{T1,1}$, $L_{T1,2}$, $L_{T1,3}$, L_{N1}, $L_{L1,1}$, $L_{L1,2}$, $L_{T2,1}$, $L_{T2,2}$, $L_{T2,3}$, $L_{T2,4}$, L_{N2}, and L_{L2} are coefficients for the effects of CO_2 fertilization, climate variability, N availability, and leaf area changes (see Appendix A). Due to the lack of historical data about changes in h_r, S_{sun}, and S_{shad} since industrialization, we omit their impacts in this study. All these L terms (shortened as L_x) and p_{can} vary diurnally and seasonally as well as between locations. Due to the covariance between L_x and p_{can}, L_x cannot be factored out of the two-dimension integration in Eq. (11). To carry out this integration, detailed data for L_x and p_{can} are required. In reality, this is not feasible, especially for the long historical periods in this study. To avoid this difficulty, we use a 3-step spatial and temporal scaling algorithm: (1) To replace the integration by a discrete summation; (2) To estimate the discrete summation using the correlation coefficient, r, between the two variables L_x and p_{can}, namely,

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

where n is the number of data points in terms of both time periods and spatial locations, $\langle L_x(i)\rangle$ is the spatial and temporal assemble average of L_x in year i, and σ is the standard deviation; and (3) To introduce a conversion coefficient, ψ_{Lx}, that gives $\langle L_x(i)\rangle = \psi_{L_x}\overline{L_x}(i)$, where $\overline{L_x}(i)$

is calculated using annual mean values of climate, N availability, and CO_2 concentration. Using this algorithm, we express term I as follows:

$$\text{Term I} = \{f_p(i)$$
$$[\zeta_{L_1,p}\psi_{L_1}\overline{L_1}(i)\Delta c_a(i)$$
$$+ \zeta_{L_{N1},p}\psi_{N1}\overline{L_{N1}}(i)\Delta N_l(i)$$
$$+ (\zeta_{L_{T1,1},p}\psi_{T1,1}\overline{L_{T1,1}}(i) + \zeta_{L_{T1,2},p}\psi_{T1,2}\overline{L_{T1,2}}(i)$$
$$+ \zeta_{L_{T1,3},p}\psi_{T1,3}\overline{L_{T1,3}}(i))\Delta T_a(i)$$
$$+ \zeta_{L_{l1,1},p}\psi_{L1,1}\overline{L_{L1,1}}(i)\Delta L_{sun}(i)$$
$$+ \zeta_{L_{L1,2},p}\psi_{L1,2}\overline{L_{L1,2}}(i)\Delta L_{shad}(i)]$$
$$+ (1 - f_p(i))$$
$$[\zeta_{L_2,p}\psi_{L_2}\overline{L_2}(i)\Delta c_a(i) + \zeta_{L_{N2},p}\psi_{N2}\overline{L_{N2}}(i)\Delta N_l(i)$$
$$+ (\zeta_{L_{T2,1},p}\psi_{T2,1}\overline{L_{T2,1}}(i) + \zeta_{L_{T2,2},p}\psi_{T2,2}\overline{L_{T2,2}}(i)$$
$$+ \zeta_{L_{T2,3},p}\psi_{T2,3}\overline{L_{T2,3}}(i)$$
$$+ \zeta_{L_{T2,4},p}\psi_{T2,4}\overline{L_{T2,4}}(i))\Delta T_a(i)$$
$$+ \zeta_{L_{L2},p}\psi_{L2}\overline{L_{L2}}(i)\Delta L_t(i)]\}\left(\frac{P(i) + P(i-1)}{2}\right)$$
$$= \chi_1(i)\left(\frac{P(i) + P(i-1)}{2}\right), \tag{13}$$

Term II in Eq. (11) is the effect of the change in forest area on the total photosynthesis. Since we consider only the existing forests, and LUC effects are outside the scope of this study. The changes in forest area due to disturbances are considered in Section 3.1.

Term III in Eq. (11) is the result of growing season length changes, i.e.

$$\text{Term III} = \frac{P(i) + P(i-1)}{l_g(i) + l_g(i-1)}\Delta l_g(i)$$
$$= \chi_3(i)\frac{P(i) + P(i-1)}{2}. \tag{14}$$

This term can be very important at high latitudes where the growing season is short and air temperature increased at a higher rate than that at low and middle latitudes (Frolking, 1997; Chen et al., 1999b). Inserting Eqs. (13) and (14) into Eq. (11), we calculate the interannual relative change in $P(i)$ by

$$\frac{\mathrm{d}P(i)}{\mathrm{d}i} = [\chi_1(i) + \chi_3(i)]\left[\frac{P(i) + P(i-1)}{2}\right]$$

$$= \chi(i)\left[\frac{P(i) + P(i-1)}{2}\right]. \tag{15}$$

So far, we have considered only gross photosynthesis rate $P(i)$. NPP is only about 25–60% of $P(i)$, dependent on plant species, because a large part of $P(i)$ is consumed by autotrophic respiration (Ryan et al., 1997). Yet, the ratio of NPP to $P(i)$ is conservative with climate change and N status (Ryan et al., 1997), so that

$$\frac{\mathrm{dNPP}(i)}{\mathrm{NPP}(i)\mathrm{d}i} = \frac{\mathrm{d}P(i)}{P(i)\mathrm{d}i}. \tag{16}$$

From Eq. (1) and Eqs. (15) and (16), the effects of non-disturbance factors on NPP can then be calculated as

$$\phi_{\mathrm{NPP}n}(i) = \prod_{j=1}^{i} \frac{2 + \chi(j)}{2 - \chi(j)}. \tag{17}$$

3.3. N cycle and leaf N content

The total available N in the soils in year i, $N_{av,s}(i)$, is the sum of atmospheric N deposition $N_{\mathrm{dep}}(i)$, biotic N fixation $N_{\mathrm{fix}}(i)$, and net N mineralization $N_{\min}(i)$

$$N_{av,s}(i) = N_{\mathrm{dep}}(i) + N_{\mathrm{fix}}(i) + N_{\min}(i). \tag{18}$$

We use measured $N_{\mathrm{dep}}(i)$ values (Ro et al., 1995). The value of $N_{\mathrm{fix}}(i)$ is calculated based on the studies of Van Cleve and Alexander (1981), Parton et al. (1987), and Chapin and Bledsoe (1992) (see detail in Chen et al., 2000b). Net N mineralization is stochastically related to the C cycle through the C/N ratios and is calculated by:

$$N_{\min}(i)$$

$$= \frac{\Lambda(i)(k_{\mathrm{cd},a} + k_{\mathrm{cd},m} + k_{\mathrm{cd},s})C_{\mathrm{cd}}(i)}{CN_{\mathrm{cd}}(i)}$$

$$+ \frac{\Lambda(i)(k_{\mathrm{fd},a} + k_{\mathrm{fd},m} + k_{\mathrm{fd},s})C_{\mathrm{fd}}(i)}{CN_{\mathrm{fd}}(i)}$$

$$+ \frac{\Lambda(i)(k_{\mathrm{md},a} + k_{\mathrm{md},m})C_{\mathrm{md}}(i)}{CN_{\mathrm{md}}(i)}$$

$$+ \frac{(\Lambda(i)k_{m,a} + \Lambda(i)k_{m,s} + k_{m,p})C_m(i)}{CN_m(i)}$$

$$+ \frac{(\Lambda(i)k_{s,a} + k_{s,p})C_s(i)}{CN_s(i)}$$

$$+ \frac{\Lambda(i)(k_{p,a} + k_{p,m})C_p(i)}{CN_p(i)}$$

$$- \frac{\Lambda(i)(k_{\mathrm{cd},m}C_{\mathrm{cd}}(i) + k_{\mathrm{fd},m}C_{\mathrm{fd}}(i) + k_{\mathrm{md},m}C_{\mathrm{md}}(i) + k_{p,m}C_p(i))}{CN_m(i)}$$

$$- \frac{\Lambda(i)(k_{\mathrm{cd},s}C_{\mathrm{cd}}(i) + k_{\mathrm{fd},s}C_{\mathrm{fd}}(i) + k_{m,s}C_m(i))}{CN_s(i)}$$

$$- \frac{k_{m,p}C_m(i) + k_{s,p}C_s(i)}{CN_p(i)}. \tag{19}$$

This equation follows the same principle as that of Townsend et al. (1996) and Holland et al. (1997), but differs in two aspects. One is that additional soil C pools are included in this equation. The second aspect is that we allow C/N ratios of biomass and soil C pools to vary, based on recent experimental findings. Many recent studies revealed that when grown in higher CO_2, plant issues (including green leaves) had consistently lower N concentration (e.g. Curtis et al., 1995). Yet leaf litter quality is essentially the same under different CO_2 levels because N is withdrawn prior to leaf senescence (O'Neill, 1994). In contrast, N in fine roots is not mobilized prior to senescence (Nambiar, 1987), and the C/N ratio was found to be much higher in fine roots grown under higher CO_2 environments (Norby, 1994). Experimental evidence also showed that C/N ratios of soil C pools vary from year to year (Schimel et al., 1994), and vary at different N and CO_2 levels (Pregitzer et al., 1995). Some recent models (e.g. Schimel et al., 1996; Comins, 1997) have incorporated these experimental findings of varying C/N ratios. In this study, we calculate a C/N ratio for each of the biomass and soil C pools as the ratio of total C content to total N content of the C pool in the year of concern.

Due to N loss as a result of wildfire, harvest, gas emission, and leaching, only a fraction of $N_{av,s}(i)$ will be taken up by the plants. The value of $N_{\mathrm{up}}(i)$ can be determined through solving three related equations: (1) $N_{av,s}(i) = N_{\mathrm{up}}(i) + N_{\mathrm{loss}}(i)$; (2) a Michaelis–Menten relationship between

$N_{up}(i)$ and the inorganic N concentration in the soil (Rastetter et al., 1991; Hudson et al., 1994); and (3) a linear relationship between $N_{loss}(i)$ and the inorganic N concentration in the soil. The solution for $N_{up}(i)$ is given by:

$$N_{up}(i) = \frac{N_{up,max}(i)}{1 + \dfrac{2N_{av,s}b_2}{N_{av,s} - N_{up,max}(i) - b_2} + \sqrt{(N_{av,s} - N_{up,max}(i) - b_2)^2 + 4N_{av,s}b_2}}, \quad (20)$$

where the maximum uptake capacity $N_{up,max}(i)$ is given by $b_1[C_{fr}(i)/C_{fr}(0)]$ $[CN_{fr}(i)/CN_{fr}(0)]$-$Q_{10,Nup}^{(T_s(i) - T_s(0))/10}$, b_1 and b_2 are constants determined by equaling N input into and export from the forest ecosystems during the pre-industrial periods. In addition to the $N_{up}(i)$, the N transferred from senesced leaves in year $i - 1$, $N_{tr}(i)$, also contributes to the total available N in plants in year i, $N_{av,p}(i)$.

We use the same coefficients partitioning $N_{av,p}$ to green leaf, fine roots, wood, and coarse roots in year i as in year $i - 1$ because there is no evidence that these coefficients vary in one way or another. Equations for calculating C/N ratio of green leaf, fine roots, wood, coarse roots, fine structure detritus, coarse structure detritus, and slow soil C are given in Appendix A. The C/N ratios of microbe, metabolic detritus, passive soil C, and charcoal are assumed to be constant. With the known values of $CN_l(i)$ and $L_t(i)$, and $C_l(i)$, the mean leaf N content per unit leaf area at year i, $N_l(i)$, can be calculated as follows

$$N_l(i) = \frac{C_l(i)}{CN_l(i)L_t(i)}, \quad (21)$$

where the value of $N_l(i)$ is constrained to $\leq N_{lmax}(i)$. Since the relationship between age and NPP is empirically pre-determined, the interactions between changes in NPP caused by age class shift and N cycle have already been included in the age–NPP relationship. Therefore, the value of $N_l(i)$ is calculated after considering only the climatic and atmospheric changes.

3.4. C cycle

The change in the size of each C pool in InTEC is described by the first-order rate kinetics (Paul and Clark, 1996)

$$\Delta C_x(i) = \text{Input}(i) - k_x(i)C_x(i), \quad (22)$$

where Input(i) is a fraction of NPP transferred to biomass C pools or a fraction of upstream C pools to soil and forest product C pools. It is important to note that if inventory-based $C_x(i)$ and estimated NPP are used, which can only be measured or estimated with limited accuracy, a large error can be introduced in $\Delta C_x(i)$, which is usually much smaller than NPP or $k_x(i)C_x(i)$ in a given year. To avoid this error, we rearrange Eq. (22) by taking $C_x(i)$ as $C_x(i - 1) + \Delta C_x(i)$, so that

$$\Delta C_x(i) = \frac{\text{Input}(i) - k_x(i)C_x(i - 1)}{1 + k_x(i)}. \quad (23)$$

To calculate $C_x(i - 1)$, $C_x(i - 2)$ and NPP$(i - 1)$ are needed. This procedure continues, until the pre-industrial period is reached during which we assume $\Delta C_x(0) = 0$ under the mean disturbance rates and climatic and atmospheric conditions. This procedure shows that $\Delta C_x(i)$ depends on historical changes in disturbance rates and climatic conditions over the entire time period since the industrialization. Following this procedure, the changes in biomass, soil, and forest products C pools are calculated by subtracting C output terms (i.e. transfer to downstream pools, and fire emission, oxidation, and respiration to the atmosphere) from the input terms (i.e. fraction of NPP partitioned to the C pool concerned, and C transfer from upstream pools). Farquhar and Henry (1997) estimated that $\sim 10\%$ of remaining wood after burning will become charcoal instead of C_{cd}, and we adopt this percentage in this study. The value of $F_m(i)$ affects the partitioning of leave and fine roots litter to detritus C pools, and is given by $F_m(i) = 0.85 - 0.018LN(i)$ (Schimel et al., 1996). Equations for calculating changes in biomass, soil, and forest products C pools are given in Appendix A. For the five product pools, the changes in the sizes of lumber ($\Delta C_{lu}(i)$), pulp-wood ($\Delta C_{pw}(i)$), and landfills ($\Delta C_{lf}(i)$) C pools are calculated also using the first-order rate kinetics in the same way as for ecosystem C pools, while the bio-energy and burned-as-waste release C within a year.

Summation of these C pool changes gives the area-averaged annual C balance or NBP in year i. The cumulative change in each of these C pools is obtained by integrating the change since the industrialization.

4. Model application for Canada's forests

To apply the model for Canada's forests, model parameters have been calibrated using experimental data obtained from Canada's forest ecosystems (see detail in Chen et al., 2000b). One modification made to these parameters is allowing f_p to change with LAI (Fig. 3). The ratio shaded leave to sunlit leave increases with total LAI and the photosynthetic rate of shaded leave are usually limited electron transport, so that f_p increases with total LAI. The description of data sources of the ten external variables can be found in Chen et al. (2000a), with Figs. 4–6 showing the temporal variations of these variables, and Fig. 7 showing the spatial distribution of N deposition.

4.1. Short-term and long-term effects of each factor

To better understand the role played by each of

Fig. 4. Area of Canada's forests disturbed by forest fire, harvest, and insect-induced mortality during the period from 1800 to 1998. Measurements were available from 1920, and values before 1920 were inferred from age-class distribution in 1920 (Chen et al., 2000a).

these external factors in the C cycle, and also to facilitate model comparison and validation, the effects of each factor need to be investigated. When different time scales are concerned, the effects of each factor may be different. For example, the direct effect of fire may last only a short
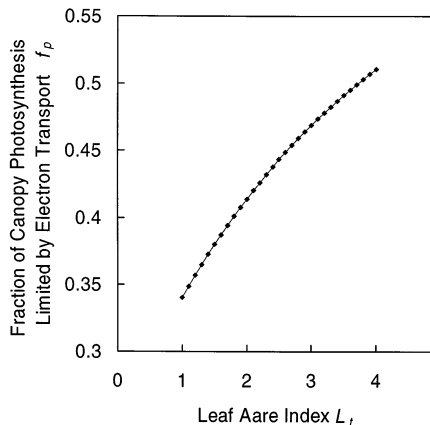

Fig. 3. Fraction of canopy photosynthesis limited by electron transpot, f_p, as a function of leaf area index, calculated using measurements made at the BOREAS old black spruce (OBS) site in 1995 and 1996, and at the old aspen (OA) site in 1994 and 1996.
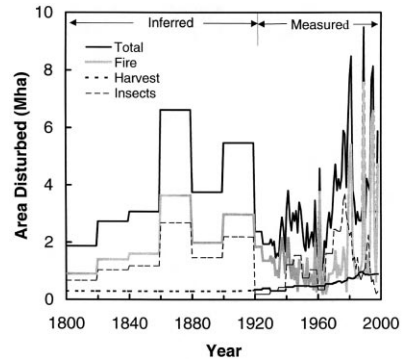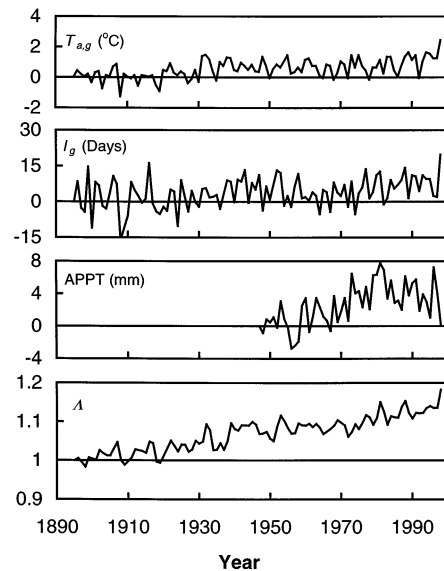

Fig. 5. National mean growing season air temperature $T_{a,g}$, growing season length l_g, and annual precipitation APPT, shown as departure relative to 1895 levels. Also shown is and abiotic decomposition factor Λ as the ratio to its 1895 value.
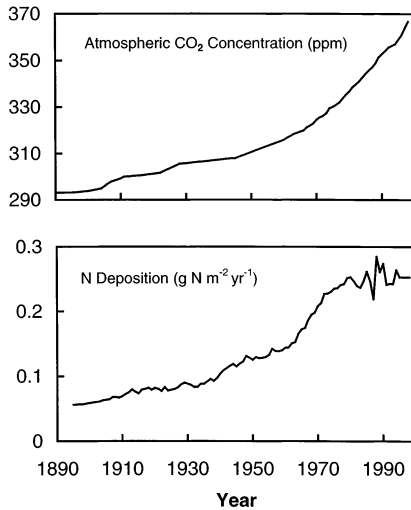
Fig. 6. Atmospheric CO_2 concentration and N deposition from 1895 to 1998. N deposition during 1984–1994 was determined based on measurements made at 30 sites across Canada (see Fig. 7), and was extended to 1895 based on the trend of national greenhouse gas emission records. The mean rate during 1984–1994 was used for 1995–1998 since the measurements indicated that N deposition had been stable since 1980s.

time period, its 'after' effect may continues for decades to centuries by altering the state variables of the forest ecosystem: the age of the forest stand disturbed and sizes of biomass and soil C pools. In this study, we define the effect on C cycle caused by a change in an external factor in the year when the change occurs as a 'short-term' effect, and the effect in years after its occurrence as a 'long-term' effect. Due to the large interannual variations in many of the external forcing factors, distinguishing between short-term and long-term effects becomes very difficult if actual historical data are used. To simplify the matter, we analyze the short-term and long-term effects for each of these factors by perturbing one of the 10 factors in year 1 since the industrialization while keeping this factor in all other years and all other factors in all years at pre-industrial levels. The perturbation study includes increases in burned area and insect-induced mortality each by 2 Mha, harvest and planting each by 0.5 Mha, $T_{a,g}$ by 1°C, l_g by 7 days, APPT by 50 mm, Λ by 5%, CO_2 by 2

ppm, and N deposition by 0.02 g N m^{-2} per year.

Fig. 8 shows the short-term and long-term effects of each factor on NPP. Because the disturbances destroy forest stands in the year when they occur, and since the forest stands regenerated thereafter grow slowly in the first 20 years, the area-averaged NPP in year 1 and the next ~ 20 years is reduced. As the regenerated forests enter more productive ages, the NPP increases, reaching a maximum around 40–60 years after disturbance, and decreasing again thereafter as the forests age. Planting eliminates the regeneration delay period, and so shifts the productive stage forward by 5–9 years (Bunce, 1989). As a result, planting increases NPP in the first ~ 50 years, and reduces it thereafter because naturally regenerated forest stands will be younger and more productive than planted stands at the later stages.

The perturbations in l_g, $T_{a,g}$, and CO_2 increase NPP significantly in the perturbation year, but reduce it in the subsequent years. Numerous measurements showed that increases in l_g and CO_2 enhanced NPP in the same year (Frolking, 1997; Wullschleger et al., 1997; Chen et al., 1999b). Yet, over a period of > 2 years, the enhancement of CO_2 was reduced even if CO_2 was maintained at the same elevated level (McKane et al., 1997; Idso, 1999), indicating the negative long-term effect of an increase in CO_2 on growth. If there were not a negative long-term effect, then the enhancement should be always the same when CO_2 was kept at the same elevated level, indifferent to the previous CO_2 concentration. This negative long-term effect has also been observed for plants growing near a natural CO_2 spring with a CO_2 concentration at ~ 790 ppm (Cook et al., 1998). Various hypotheses have been proposed to explain these variable short- and long-term effects of elevated CO_2 concentrations (Luo et al., 1999). From the perspective of C–N cycles at the ecosystem level, the long-term negative effect of increasing CO_2 can be explained through its influence on the state variables of leaf N content and leaf area. The positive short-term effect on NPP in the perturbation year results in larger leaf area and higher C/N ratios in roots and wood detritus in year 2. The higher C/N

ratios in roots and wood detritus reduce the net N mineralization rate. Both reduced net N mineralization rate and increased leaf area reduced the area-based leaf N content. Since the majority of the increased leaf area is shaded leaves, their contribution to NPP is usually not enough to compensate for the decrease in leaf N content, and consequently NPP is reduced. For the subsequent years, the reduction in the net N mineralization rate caused by higher C/N ratios in roots and wood detritus has greater negative effects on NPP. The effects of l_g and $T_{a,g}$ can be explained in the same way, except that in reality their changes are often accompanied by soil temperature changes which have effects opposite to those of l_g and $T_{a,g}$. In addition, the interannual variations in l_g and $T_{a,g}$ are usually large. As a result, the long-term effects of l_g and $T_{a,g}$ are masked by

their short-term effects, and therefore measurements that show their long-term effects are rare.

N deposition, Λ (affecting net N mineralization), and APPT (affecting N fixation) influence NPP through leaf N content, which is an ecosystem internal state variable and represents the cumulative effects of climatic and atmospheric factors over many years. As a result, perturbations in N deposition, Λ, and APPT usually modify the leaf N content only slightly in the perturbation year (depending on the amount of N added), but their effects can last for many years. For example, fertilization trials conducted during 1970s and 1980s in Canada showed that measurable growth enhancements of fertilization may last for over 10 years (Weetman et al., 1987; Gardner, 1990). For a Douglas-fir ecosystem in British Columbia, significant enhancements were
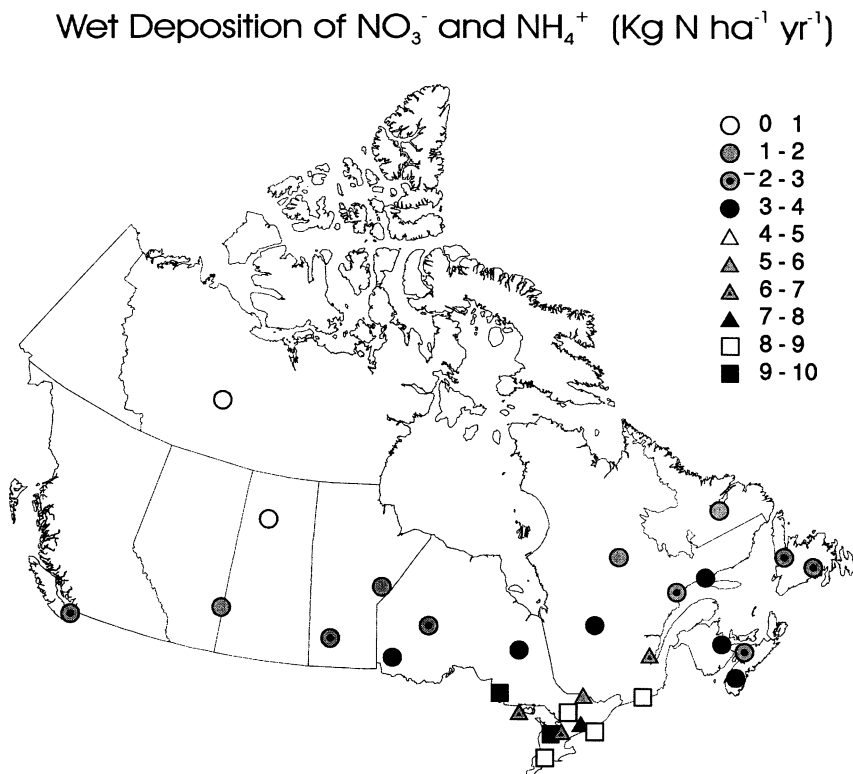

Fig. 7. Map showing the wet deposition of NO_3^- and NH_4^+ measured at 30 sites across Canada during 1984–1994.
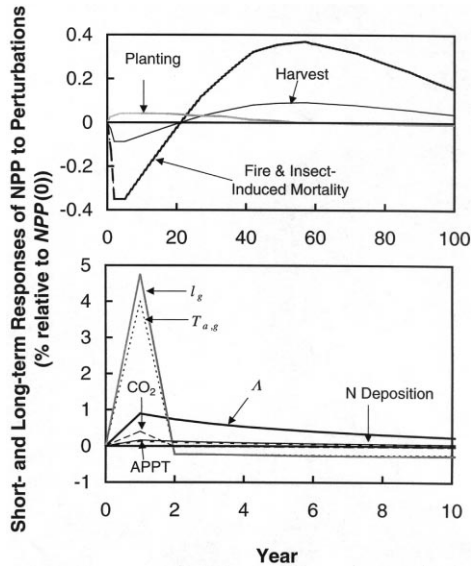
Fig. 8. Short-term long-term effects on NPP of Canada's forests by a single-year perturbation imposed on each of following ten disturbances and climatic and atmospheric factors in year 1: burned area and insect-induced mortality each increasing by 2 Mha, harvest and planting each by 0.5 Mha, mean growing season air temperature ($T_{a,g}$) by 1°C, growing season length (l_g) by 7 days, annual precipitation (APPT) by 50 mm, abiotic decomposition factor by 0.1, atmospheric CO_2 concentration by 2 ppm, and N deposition by 0.02 g N m^{-2} per year. In year 0 and all years after year 2, all factors remain at their pre-industrial levels.

measured for the period 12–15 years after the initial fertilization (Gardner, 1990).

The short-term and long-term effects of the ten disturbance and non-disturbance factors on NBP are largely similar to those on NPP (Fig. 9), except for the following three aspects: (1) The increase in annual burned area releases a substantial amount of C into the atmosphere in the year it occurs, and so has more negative short-term effect on NBP than on NPP; (2) The increase in Λ has a negative effect on NBP in the perturbation year because of the resultant increase in soil respiration, compared to a positive short-term effect on NPP; (3) For NPP, the long-term effects of these factors are achieved through altering age, C/N ratios of biomass and soil C pools, leaf area, and leaf N content. For NBP, another important ecosystem state variable, the sizes of biomass and soil C pools, is added to the list. Therefore, if the

effect of a factor on NBP is positive in years immediately after the perturbation, an additional C soil release is expected during the period thereafter, or vice versa.

4.2. Integrated effects of all 10 factors

4.2.1. NPP

As Fig. 4 shows, the disturbance rates during 1860–1920 and during 1970–1998 were high, and were low during early 1800s and 1920–1970. This temporal distribution of disturbance rates resulted in significant variations in the percentages of young and less productive stands (i.e. < 20 years old), productive stands (i.e. 20–100 years old), and old and less productive stands (i.e. > 100 years old) (Fig. 10). From 1800–1820, fire and insect-induced mortality rates were lower than their pre-industrial averages. Consequently, the percentage of young stands decreased while that of productive stands increased. The increasing disturbance rates from 1820 to 1880 reduced the percentage of productive stands to a minimum of 41% around 1880. The decreasing trends in the percentage of productive stands was reversed since then and reached a maximum of 71% in 1940, as fire and insect-induced mortality rates
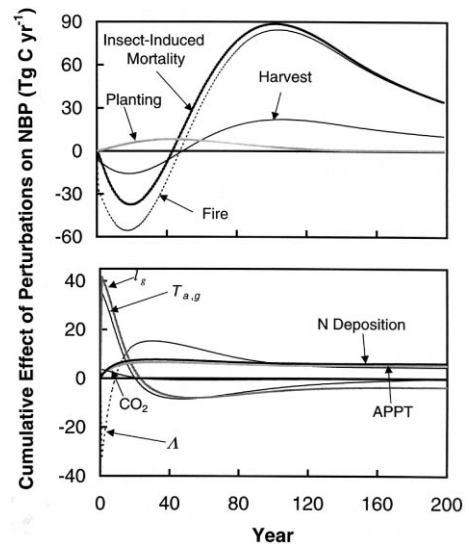

Fig. 9. Same with Fig. 8 except for the cumulative effects of perturbations on NBP of Canada's forests.
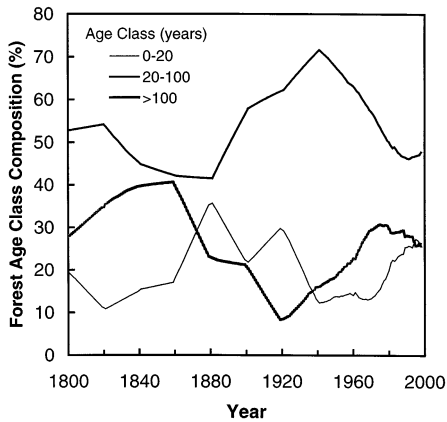
Fig. 10. Histogram of age class composition of Canada's forests from 1800 to 1998, resulted from the rate changes in fire, insect-induced mortality, harvest, and planting.

used in determining ϕ_{NPPd}, the error caused by the assumption gradually diminished. Therefore, the estimates of ϕ_{NPPd} during the 20th century should be more accurate than those during the 19th century.

As Figs. 5 and 6 shows that from 1895 to 1998, the national mean $T_{a,g}$ increased by $\sim 1°C$, l_g by 1 week, APPT by 5 mm, Λ by 14%, CO_2 concentration by 74 ppm, and N deposition by 0.2 g N m^{-2} per year. The resultant ϕ_{NPPn} increased gradually from 1895 to 1940, mainly in response to climatic changes (Fig. 12). It decreased slightly during the next three decades because of the tradeoff between the increasing N deposition effect and decreasing climatic effects. In the recent two decades, both N deposition and climatic changes increased NPP, resulting in ϕ_{NPPn} increasing faster than during 1895–1940. The effect of CO_2 was small throughout the period from 1895–1998, as its positive short-term effect being counterbalanced by its long-term negative effect.

decreased in this period. From 1940–1970, the fire and insect-induced mortality rates were still low, but the stands disturbed during 1860–1920 high rate period entered into old and less productive ages, reducing the percentage of productive stands. The increases in fire and insect-induced mortality rates during the last two decades increased the percentage of young stands substantially and reduced the percentage of productive stands further.

The resultant temporal distribution of ϕ_{NPPd} resembled that of the percentage of productive stands, because after all the later was the largest contribution to the regional mean NPP (Fig. 11). This fact indicates that the importance of the long-term effect of disturbance rates on NPP. Among these disturbance factors, fire and insect-induced mortality were the two biggest contributors. The effects of harvest and planting on NPP had been minimal until 1970s, since then their effects have become significant.

Because ϕ_{NPPd} was affected by long-term effects of disturbance rates, and the disturbance rates before 1800 were unlikely to be constants as assumed, the accuracy of ϕ_{NPPd} was expected to be low in the early part of the 19th century. As the year of interest becomes further away from 1800 and more real disturbance rates were

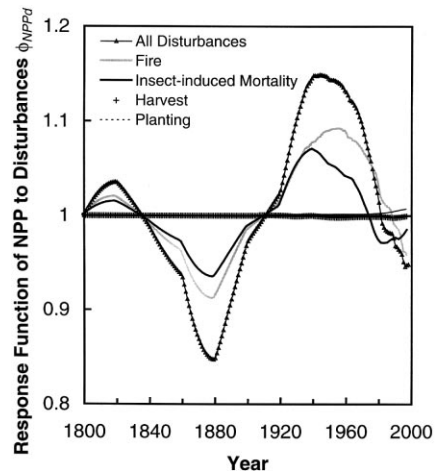Fig. 11. Response of NPP of Canada's forests to all disturbances during 1800–1998, where a ϕ_{NPPd} value of 1 indicates no effect, and 1.1 (or 0.9) indicates a 10% enhancement (or reduction). Also plotted are the responses of NPP of Canada's forests to fire, insect-induced mortality, harvest, and planting, considered individually while assuming others remain at their pre-industrial levels.
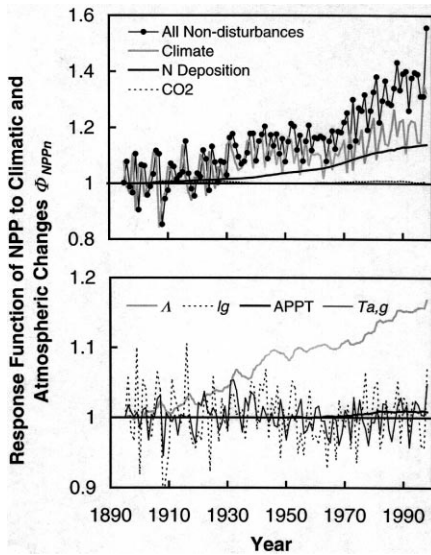
Fig. 12. Response of NPP of Canada's forests to all 'non-disturbance' climatic and atmospheric changes during 1895–1998 where $\phi_{\mathrm{NPP}n} = 1$ indicating no effect, > 1 positive effect, and < 1 negative effect. Also plotted are the responses of NPP of Canada's forests to growing season air temperature $T_{a,g}$, growing season length l_g, abiotic decomposition factor Λ, annual precipitation, CO_2, and N deposition, each of which is considered by assuming others remain at their pre-industrial levels.

When averaged over the entire period from 1800 to 1998, disturbances increased $\phi_{\mathrm{NPP}d}$ by less than 1%, with the highest contribution due to fire (Table 1). These values were calculated by allowing only the factor considered to change while all other factors were maintained at their pre-industrial levels. Insect-induced mortality was the second most important factor causing the variations in $\phi_{\mathrm{NPP}d}$, although much less on average. Harvest reduced the mean $\phi_{\mathrm{NPP}d}$ by 0.04%, whereas planting increased it by 0.1% during 1800–1998. Over the same period, $\phi_{\mathrm{NPP}n}$ increased by 8.1%. The effect of Λ on $\phi_{\mathrm{NPP}n}$ was the largest at 4.0%, followed by N deposition and CO_2 at 2.5 and 0.2% respectively, while the other three were all less than 0.1%. If only Λ changed and all other factors remained at their pre-industrial levels, the net N mineralization rate would have increased by 5.5% from 1800 to 1998. With actual climatic and atmospheric data, the net N mineralization rate increased by 2.9% for the same period (Fig. 13).

The ~ 1.8 g N m^{-2} per year net N mineralization rate was the largest component of available N for plants in Canada's forest ecosystems, similar to findings for other mid-high latitude forest ecosystems (Aber and Driscoll, 1997). Observed rates of net N mineralization cited by Bonan (1990) ranged from 0.8 to 5.8 g N m^{-2} per year: 0.8–1.8 g N m^{-2} per year in mature black spruce forests (*Picea mariana* (Mill.) B.S.P) in the upland of interior Alaska; 1.1 g N m^{-2} per year in a black spruce forest in central Quebec; 1.7–2.0 g N m^{-2} per year in mature white spruce forests (*Picea glauca* (Moench) Voss) in the upland of interior Alaska; and 2.4–5.8 in mature birch forests (*Betula papyrifera* Marsh.) in the upland of interior Alaska. Our result was in the range of these observations, especially close to those in spruce forests, which are the dominant species of Canada's forests.

After integrating the short-term and long-term effects of all disturbance and non-disturbance factors, we found that the national mean NPP of Canada's forests increased slightly during 1800–

Table 1
Averaged effects of disturbances and climatic and atmospheric changes on NPP[a]

	1800–1998	1990–1998
Fire	0.79	−2.4
Insects	0.11	−2.1
Harvest	−0.04	−0.1
Planting	0.10	0.6
Disturbances	**0.85**	**−4.3**
$T_{a,g}$	0.09	0.8
l_g	0.06	3.6
Λ	3.99	15.6
APPT	0.07	1.0
CO_2	0.21	0.6
N deposition	2.50	12.1
Non-disturbances	**8.1**	**39.1**
Integrated effect	**9.30**	**32.2**

[a] The effects on NPP are shown as percentages relative to its pre-industrial level. The effects of each individual factor are calculated by assuming all other factors remained at their pre-industrial levels. The effects of disturbances (or non-disturbances) are calculated by assuming all non-disturbance factors (or disturbance factors) remained at their pre-industrial levels. The final values integrate both short- and long-term effects of all factors.
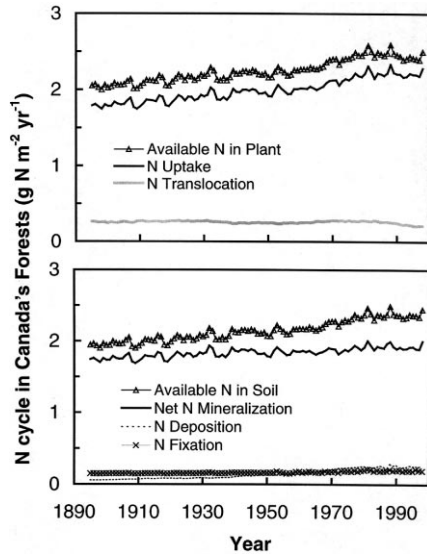
Fig. 13. Available N in soil and in plant, during 1895–1998. Available N in soil is the sum of net N mineralization, N deposition, and N fixation, while available in plant is the sum of N uptake and N retranslocation from the senescing leaves in the previous year.

1820, decreased during 1820–1880, increased again from 1880 to 1940, and remained at this level since then (Fig. 14).

4.2.2. NBP

Fig. 14 also shows that the total C loss (i.e. sum of soil heterotrophic respiration, fire emission, and forest product oxidation) remained approximately at the same level, during 1800–1820 as a result of tradeoff between decrease in fire emission and increase in soil respiration. The same was true during 1820–1900 except as a result of tradeoff between an increase in fire emission and decrease in soil respiration. After 1900, total C loss increased because of the increases in Λ and soil C stock from increasing NPP. As the residue of NPP and the total C loss, the NBP of Canada's forests was 40 ± 20 Tg C per year (i.e. a sink) in 1810s, reduced to -131 ± 66 Tg C per year (i.e. a source) in 1870s, increased thereafter to a maximum of 200 ± 100 Tg C per year in 1930s, and decreased again to 57 ± 29 Tg C per year in 1990s. The uncertainties of $\sim 50\%$ of these values are given based on a previous sensitivity analysis,

which considered both errors from NPP calculation and in original data of disturbances and climatic and atmospheric variables (Chen et al., 2000a).

Among the four disturbance factors, fire had the most important contribution to the interannual and decadal variations of NBP, followed by insect-induced mortality (Fig. 15). Our estimates of disturbance effects are similar to those of Kurz et al. (1995) for the period of 1920–1989, if the same assumptions are made (Chen et al., 2000a). For non-disturbance factors, N deposition was the largest contributor to NBP on average, while most of the interannual variations in NBP were caused by climatic factors (Fig. 16). N saturation has been observed in Central and Eastern Europe and Northeast United States (Aber et al., 1989). Based on the measurement of N deposition across Canada (Fig. 7) and the established criteria (Baron et al., 1994), N saturation has not been a problem for Canada's forests. The same conclusion was also reached by the Acid Rain National Early Warning System, which did not detect any sign of pollution damage in boreal forests (Hall,
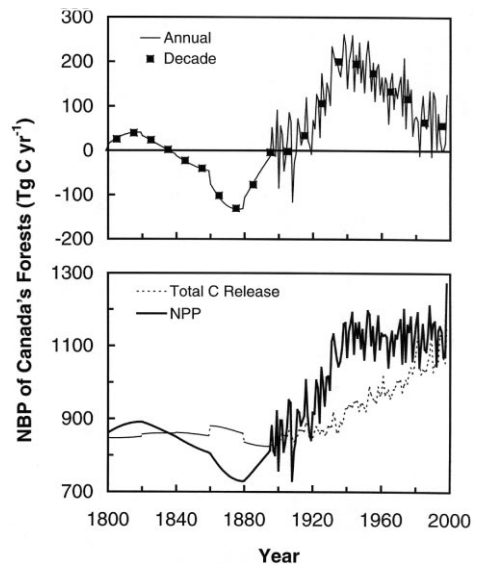

Fig. 14. Annual and decadal NBP of Canada's forests, after integrating the short- and long-term effects of disturbances and climatic and atmospheric changes, during 1800–1998. Also plotted are annual total C gain (i.e. NPP) and annual total C loss (soil respiration, fire C emission, and product oxidation).
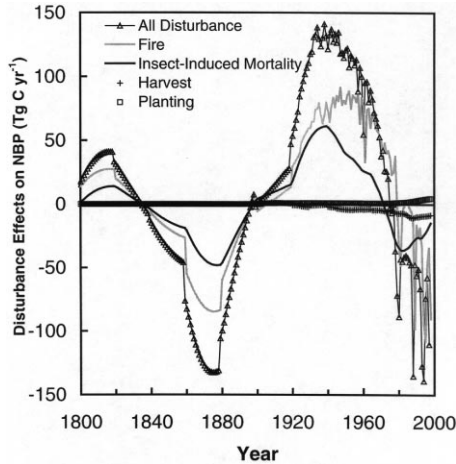
Fig. 15. Effect of disturbance factors on NBP of Canada's forests during 1800–1998. Also included are the effects of fire, insect-induced mortality, harvest, and planting on NBP of Canada's forests, each of which is considered by assuming others remain at their pre-industrial levels.

1995). Overall, the contribution of CO_2 to NBP was small, because of the counterbalance between the positive short-term effect and negative long-term effect of increases in CO_2 concentration. During 1910–1930 and 1960–1998 CO_2 increased at fast rates, consequently its short-term effect outbalanced its long-term effect and a relative large CO_2 contribution was found. These results are consistent with findings from studies which considered coupled C–N cycles, such as TEM (McGuire et al., 1992; Melillo et al., 1993). Melillo et al. (1993) found that the response in tropical and dry temperate ecosystems was dominated by CO_2, but those in northern and moist temperate ecosystems reflected the effects of temperature on N availability. The underlying reason for this is that most ecosystems, except for some tropical ecosystems, are N limited, and the limitation is greater at higher latitudes (McGuire et al., 1992).

Averaged over the entire period during 1800–1998, NBP was 40 Tg C per year. N deposition was the largest contributor by $\sim 36\%$, followed by Λ by $\sim 20\%$ and fire by $\sim 17\%$. The contributions of other factors were less than 10%, with a remaining 9% due to interactions between all these effects (Table 2). These partitioning percent-
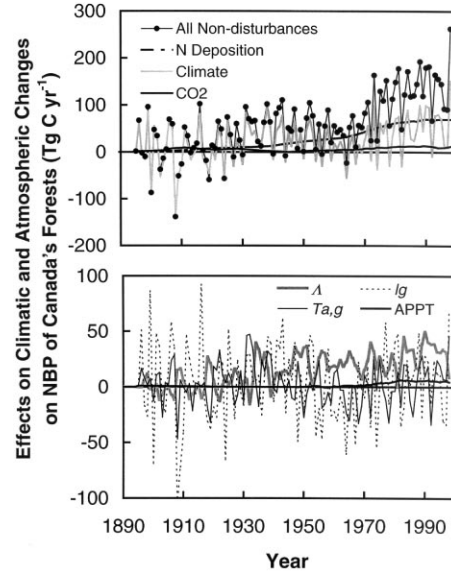

Fig. 16. Effect of 'non-disturbance' climatic and atmospheric factors on NBP of Canada's forests during 1800–1998. Also included are the effects of growing season air temperature $T_{a,g}$, growing season length l_g, abiotic decomposition factor Λ, annual precipitation, CO_2, and N deposition, when each of them is considered by assuming others remain at their pre-industrial levels.

ages changed for different time periods. In 1990s, the effect of N deposition of ~ 70 Tg C per year exceeded the magnitude of NBP by ~ 57 Tg C per year (Table 2). Again, a simple summation of all these effects would have overestimated NBP by

Table 2
Same as Table 1 except for NBP (Tg C per year)

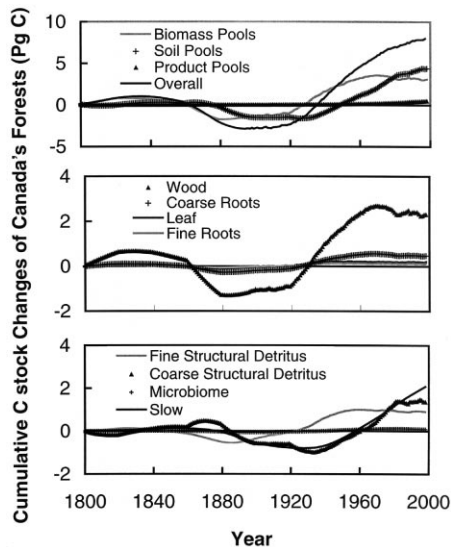|	1800–1998	1990–1998
Fire	6.7	− 52.0
Insects	1.7	− 22.7
Harvest	− 1.8	− 9.2
Planting	0.6	3.7
Disturbances	**6.7**	**− 81.1**
$T_{a,g}$	1.3	11.3
l_g	1.5	25.8
Λ	7.9	13.5
APPT	0.8	1.7
CO_2	3.2	11.3
N deposition	14.3	70.0
Non-disturbances	**31.9**	**149**
Integrated effect	**39.7**	**57.1**

Fig. 17. Cumulative stock changes of Canada's forest C pools since 1800: overall, soil, biomass, and products, as well as individual soil and biomass C pool.

28%, demonstrating the necessity of integrated analysis.

4.2.3. C stock

The cumulative stock changes of C pools in Canada's forests as a result of changes in disturbance rates and climatic and atmospheric conditions are shown in Fig. 17. A time lag between the C stock change in biomass and that in soil was clearly evident here. The biomass C stock started to increase gradually around 1880, whereas that of soil did not increase until around 1930. Around 1970, the biomass C stock decreased slightly and stabilized thereafter, while soil C stock continued to increase. The primary reason for this time lag was the differences in the ways biomass and soil C pools respond to disturbances and climatic and atmospheric changes. For example, fire, insect-induced mortality, and harvest reduced biomass C stock, but increased soil C stock in the disturbance year through transferring biomass C to soil. Over the decades after the disturbances, however, biomass was restored gradually, yet soil C stock would continue to decline for up to ~50 years before it started to recover again. Increasing Λ

resulted in immediate C loss from soil, but enhanced NPP and biomass C stock. It would be many years before the increased biomass C stock would be transferred to soil. All other climatic and atmospheric factors increased first the biomass C stock, which would be transferred to soil C pools many years later. Such time lag was also found between detritus C pools and slow soil C pool, because the later was at the lower end the carbon transfer cascade.

For biomass, the largest C stock change occurred in the wood pool, since it was the largest among biomass C pools. Yet, although the passive soil C pool was largest among soil C pools, its extremely long residence time made it inert to changes. The largest soil C stock changes occurred in detritus and slow soil C pools. Averaged over the entire period from 1800 to 1998, the slow soil C pool accounted for 47% of the C stock change in soil, followed by coarse and fine structural detritus at 31 and 21%, respectively (Table 3). Overall, the soil C stock increased 4.321 Pg from 1800 to 1998, or 2.1% of the current soil C stock of 206.5 Pg, while the above-ground biomass increased 2.473 Pg, or 19.1% of current

Table 3
Cumulative stock changes of Canada's forest biomass, soil, and product C pools for periods during 1800–1998 and during 1990–1998

	1800–1998 (Pg C)	1990–1998 (Pg C)
Wood	2.273	−0.041
Leaves	0.208	0.011
Fine roots	0.130	0.012
Coarse roots	0.438	−0.006
Biomass	**3.089**	**−0.024**
Coarse detritus	1.359	−0.011
Fine detritus	0.905	0.017
Charcoal	−0.001	0.024
Microbe	0.089	−0.018
Slow	2.051	0.428
Passive	−0.084	−0.007
Soil	**4.321**	**0.434**
Lumber wood	0.278	0.065
Pulp wood	0.064	0.008
Landfill	0.138	0.034
Products	**0.479**	**0.106**
Total	**7.889**	**0.516**

inventory-based value of 13 Pg. During the 1990s, the aboveground biomass C stock, however, decreased by 0.4% of its current total (Table 3). With the accuracy of forest volume inventory data being $\sim 6\%$ (Auclair and Bedford, 1997), such a small variation in aboveground biomass C stock cannot be detected using forest volume inventory techniques. Table 3 also shows that the soil C stock during 1990s increased by 0.434 Pg, or on average at the rate of 11.5 g C m^{-2} per year, which is consistent with recent Boreal Ecosystem-Atmosphere Study (BOREAS) site measurements (Nakane et al. 1997; Trumbore and Harden, 1997). Nakane et al. (1997) estimated that the soil of a black spruce forest stand near the south boreal boundary in Saskatchewan was accumulating C at 3–13 C m^{-2} per year. At another BOREAS site near the northern boreal boundary, Trumbore and Harden (1997) found that the soil of a black spruce stand was accumulating C at rate of 3–30 C m^{-2} per year, dependent on drainage conditions.

5. Concluding remarks

This study presents a regional forest C-budget model, InTEC, which integrates the effects of disturbance and non-disturbance factors. Disturbance factors considered include fire, insect-induced mortality, and harvest. Planting is also included here. Non-disturbance factors include l_g, $T_{a,g}$, APPT, and Λ, CO_2, and N deposition. Four biomass C pools (i.e. leaf, coarse root, and fine roots), seven soil C pools (i.e. coarse structural detritus, fine structural detritus, metabolic detritus, microbe, slow, charcoal, and passive), and five product C pools (i.e. lumber, pump-wood, bio-energy, burned-as-waste, and landfills) are considered.

InTEC is based on the Farquhar's leaf photosynthesis model, the Century C cycle model, the net N mineralization model of Townsend et al. (1996) and Holland et al. (1997), and an age–NPP relationship derived from forestry inventory-based age–biomass relationships. To integrate these models and relationships developed for different purposes and for different spatial and temporal scales into a coherent model, we (1) develop a spatial and temporal up-scaling algorithm for annual and regional calculations using leaf level models; and then (2) combine the upscaled results with an age–NPP relationship derived from forestry inventory-based age–biomass relationships to obtain the annual NPP of a forest region.

The C balance of a forest region is usually only a few percent of fluxes involved (e.g. NPP, soil respiration), and the percentage changes in the various C pools are even smaller. Because these fluxes or C pool sizes can only be evaluated with limited accuracy, estimates of the C balance from a single-year data of these fluxes or C pool sizes are often degraded by large uncertainties. To avoid this type of uncertainty, we use a historical change approach, in which the C balance is determined from the changes in the disturbances and non-disturbances factors, and is assumed to be at the equilibrium state under the mean pre-industrial conditions of these disturbances and non-disturbances factors. Using the historical change approach not only improves the accuracy of the past and present regional forest C balance estimates, but also enables us to predict the future regional forest C balance for projected changes in disturbance rate, climate, and atmospheric conditions. Both present estimates and future predictions of regional forest C balance are critical in formulating mitigation and adaptation strategies for global changes.

The short-term (i.e. in the perturbation year) effects of increases in fire, insect-induced mortality, and harvest on NPP and NBP are negative. Planting has little short-term effects on NPP and NBP. The short-term effects of increases in l_g, $T_{a,g}$, APPT, CO_2, and N deposition increase NPP and NBP, while increase in Λ increases NPP but reduces NBP. The long-term (i.e. in years after the perturbation) effects of increases in fire, insect-induced mortality, and harvest reduce NPP and NBP in the first 20 years after disturbances, then increase them to a maximum around 40–60 years after disturbances, and the positive effects on NPP decline afterwards. Through shifting the age-growth curve by 5–9 years, planting increases NPP and NBP in the first 40–50 years and reduces them thereafter. The long-term effects of

increases in l_g, $T_{a,g}$, and CO_2 reduce NPP and NBP, whereas those in Λ, APPT and N deposition increase them. The short-term effects directly change photosynthesis (CO_2, l_g, $T_{a,g}$), N availability (APPT and N deposition), respiration rate (Λ), and C transfer and emission rates (disturbances) in the perturbation year, while the long-term effects on NPP and NBP are realized through modifying internal ecosystem state variables, including age class, leaf N content, leaf area, and soil C stock. These state variables represent cumulative effects of external forcing factors, and so any perturbation to them require a very long time to respond fully.

Most of the Free Air CO_2 Enrichment (FACE) studies were designed to quantify the short-term and long-term responses of vegetation to double CO_2 conditions. To maintain such studies are expensive, and the results from year 2 afterwards are in fact a complex mixture of short-term and long-term effects. A more cost-efficient, and easy-to-interpret alternative is a perturbation study: enriching CO_2 in one year and returning it to the original level for more years as desired. Perturbation studies can also serve as a means for model comparison and validation, both of which are critical in order to obtain accurate regional and global C budgets (Rastetter, 1996).

Using the historical data of disturbances during 1800–1998, and climatic and atmospheric variables during 1895–1998, we estimate the integrated effects of all these external forcing factors and draw the following conclusions on the C budget of Canada's forests.

During 1800–1998, the relative importance of each factor varied from year to year. Overall, fire was the most important disturbance factor influencing NPP and NBP of Canada's forest, followed by insect-induced mortality. The effects of harvest and planting were small in 19th century, but increased in recent decades. Most of the inter-annual variability in NBP was caused by fire and climatic variables, while N deposition was the most important non-disturbance factor when averaged over the entire period 1800–1998. CO_2 contributed significantly to NBP during 1910–1930 and during 1960–1998, during which CO_2 increased at fast rates.

The annual mean NBP of Canada's forests during 1810s was 40 ± 16 Tg C per year (i.e. a sink), reduced to -131 ± 52 Tg C per year by the 1870s (source), increased thereafter to a maximum of 200 ± 80 Tg C per year by the 1930s, and decreased again since then. During 1980–1998, the negative effects of disturbance rate increases and the positive effects of non-disturbance climatic and atmospheric changes were nearly in balance, resulting in an almost constant NBP (sink) of 65 ± 26 Tg C per year in 1980s and of 57 ± 23 Tg C per year in 1990s.

During the entire period from 1800 to 1998, biomass, soil, and product C stocks increased by ~ 3.1, 4.3, and 0.5 Pg, respectively. The changes in aboveground biomass and soil C pools represented $\sim 19\%$ and $\sim 2\%$ increases, relative to their current inventory values.

Although we have made great efforts to include in InTEC all known factors affecting terrestrial C cycle, some less well understood factors, such as ozone, soil degradation, are not considered in this study. The effect of hydrological cycle is well known at the stand level, but is difficult to be incorporated at a regional scale model. High-resolution topographical maps are needed in order to consider the hydrological effects, and it represents a major challenge for the next step. The lack of data about historical changes in forest species composition prevents its inclusion in InTEC. The LUC effect can be very important in a regional C budget, and so deserves a separate study.

Notation

symbol	definition and unit
A_d, A_f, A_t	disturbed forest area, burned forest area, total forest area (m²)
APPT	annual precipitation mm
b_1, b_2	coefficients for partitioning available N into N uptake and N loss
c_i, c_a	intercellular and atmospheric CO_2 concentration µmol mol⁻¹
CN, LN	C/N ratio, Lignin to N ratio
C_x	C content in pool x (subscript) (g C m⁻²)
F_m	partitioning fraction of leaf and fine-root litterfall to metabolic detritus C pool

$F_{NPP}(y)$	normalized NPP as a function of age y	R	gross respiration rate (g C m^{-2} s^{-1})
f_p	fraction of p_{can} limited by p_{can1}	S	above-canopy photosynthetic active radiation (PAR) (μmol photon m^{-2} s^{-1})
f_x	NPP allocation coefficient to pool x		
$G(\theta)$	leaf projection coefficient	S_{sun}, S_{shad}	absorbed PAR by sunlit and shaded leaves μmol photon m^{-2} s^{-1})
h_r	air relative humidity %		
J, J_m	electron transport rate and its maximum μmol electron (m^{-2} s^{-1})	T_s, T_a	soil and air temperature (°C)
		V_m	maximum carboxylation rate (μmol CO$_2$ m^{-2} s^{-1})
J_{sun}, J_{shad}	J for sunlit and shaded leaves μmol electron (m^{-2} s^{-1})	VPD	air water vapour deficit (kPa)
k_{co}	coefficient associated with enzyme kinetics (μmol mol^{-1})	$\zeta_{L_x, p_{can}}$,	scaling factor accounting for the effect of diurnal and seasonal variations in L_x and P_{can} on dp_{can}/p_{can}
$k_{x,y}$	C transfer coefficient from pool x to y per year		
L_x	coefficients accounting for the climatic and atmospheric changes on NPP	ψ_{L_x}	ratio of assemble average of L_x calculated using half-hourly environmental conditions to L_x calculated using annual mean environmental conditions
L_t, L_{sun}	total and sunlit leaf area index (m^2 m^{-2})		
L_{shad}	shaded leaf area index (m^2 m^{-2})	η	total wood C removed due to harvest per year (g C per year)
l_g	growing season length day		
N_{av}, N_{dep}	available N, N deposition (g N m^{-2} per year)	Λ	abiotic decomposition factor
		ϕ_{NPPd},	response functions of NPP to changes in disturbance rates, and 'non-disturbance' climatic and atmospheric changes
N_{fix}, N_{min}	N fixation, net N mineralization (g N m^{-2} per year)	ϕ_{NPPn},	
N_{up}, N_{loss}	N uptake, and N loss (g N m^{-2} per year)		
N_{tr}	N transfer from previous year's senesced leaves (g N m^{-2} per year)	Γ	CO$_2$ compensation point without dark respiration (μmol mol^{-1})
		α	ratio of c_i to c_a
N_l, N_{lmax}	actual and optimal leaf N content per unit leaf area (g N m^{-2})	Ω	leaf clumping factor
		χ	relative change rate of P as a function of changes in non-disturbance factors
NPP	net primary productivity (g C m^{-2} per year)		
$P(\theta)$	gap fraction at view zenith angle θ	ξ_x	C loss from pool x due to fire (g C m^{-2} per year)
$P(i)$	mean annual gross photosynthesis rate (g C m^{-2} per year)		
p, p_1, p_2	instantaneous leaf gross photosynthesis rate, and that limited by electron transport and rubisco activity (g C m^{-2} s^{-1})	Subscript denoting C pools	
		a, cr, fr, l	Atmosphere, coarse root, fine root, leaf
P_{can}	instantaneous canopy gross photosynthesis rate (g C m^{-2} s^{-1})	w, cd, cc	Wood, coarse structural detritus, charcoal
q	mean occurrence frequency of fire and insect-induced mortality, per year	fd, md, m	fine structural detritus, metabolic detritus, microbe
		p, s, lu, pw, lf	passive soil, slow soil, lumber, pump-wood, landfill

Appendix A. Equations for calculating L_x, C/N ratio, and ΔC_x

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

$$L_{T1,1} = -0.056 c_a L_1, \tag{A2}$$

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

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

$$L_{N1} = \frac{J_m L_{\text{sun}}}{J N_l L_t} \left[0.714 - \frac{0.714 J_m - 0.1086 S_{\text{sun}}}{\sqrt{(J_m + 0.38 S_{\text{sun}})^2 - 1.064 J_m S_{\text{sun}}}} \right]$$
$$+ \frac{J_m L_{\text{shad}}}{J N_l L_t} \left[0.714 - \frac{0.714 J_m - 0.1086 S_{\text{shad}}}{\sqrt{(J_m + 0.38 S_{\text{shad}})^2 - 1.064 J_m S_{\text{shad}}}} \right], \tag{A5}$$

$$L_{L1,1} = \frac{J_{\text{sun}}}{J L_t} \tag{A6}$$

$$L_{L1,2} = \frac{J_{\text{shad}}}{J L_t} \tag{A7}$$

$$L_2 = \frac{\alpha(k_{\text{co}} + \Gamma)}{(\alpha c_a - \Gamma)(\alpha c_a + k_{\text{co}})}, \tag{A8}$$

$$L_{T2,1} = -\frac{0.056 \Gamma(\alpha c_a + k_{\text{co}})}{\alpha(k_{\text{co}} + \Gamma)} L_2, \tag{A9}$$

$$L_{T2,2} = -\frac{(0.074 k_{\text{co}} - 0.291\Gamma)(\alpha c_a - \Gamma)}{\alpha(k_{\text{co}} + \Gamma)} L_2, \tag{A10}$$

$$L_{T2,4} = 0.0875 - \frac{26461.9}{(T_a + 273)^2 (1 + e^{\frac{3147.7 - 85.4 T_a}{T_a + 273}})}, \tag{A11}$$

$$L_{N2} = 1/N_l, \tag{A12}$$

$$L_{L2} = 1/L_t. \tag{A13}$$

$$CN_l(i) = \frac{C_l(i-1) + f_l E_{\mathrm{NPP}n}(i)\,\mathrm{NPP}(0)}{\dfrac{C_l(i-1)}{CN_l(i-1)} + \dfrac{f_l}{CN_l(i-1)}\dfrac{N_{\mathrm{av},p}(i)}{\dfrac{f_l}{CN_l(i-1)} + \dfrac{f_{\mathrm{fr}}}{CN_{\mathrm{fr}}(i-1)} + \dfrac{f_w + f_{\mathrm{cr}}}{CN_w(i-1)}}}, \tag{A14}$$

$$CN_{\mathrm{cr}}(i) = CN_w(i) = \frac{C_w(i-1) + f_w E_{\mathrm{NPP}n}(i)\,\mathrm{NPP}(0)}{\dfrac{C_w(i-1)}{CN_w(i-1)} + \dfrac{f_w + f_{\mathrm{cr}}}{CN_w(i-1)}\dfrac{N_{\mathrm{av},p}(i)}{\dfrac{f_l}{CN_l(i-1)} + \dfrac{f_{\mathrm{fr}}}{CN_{\mathrm{fr}}(i-1)} + \dfrac{f_w + f_{\mathrm{cr}}}{CN_w(i-1)}}}, \tag{A16}$$

$$CN_{\mathrm{cd}}(i) = \frac{C_{\mathrm{cd}}(i-1) + k_{w,\mathrm{cd}}C_w(i) + k_{\mathrm{cr},\mathrm{cd}}C_{\mathrm{cr}}(i) + \dfrac{A_d(0)(C_w(i) + C_{\mathrm{cr}}(i)) - \xi_w A_f(0) + \eta(0)}{A_t}}{\dfrac{C_{\mathrm{cd}}(i-1)}{CN_{\mathrm{cd}}(i-1)} + \dfrac{k_{w,\mathrm{cd}}C_w(i) + k_{\mathrm{cr},\mathrm{cd}}C_{\mathrm{cr}}(i)\dfrac{A_d(0)(C_w(i) + C_{\mathrm{cr}}(i)) - \xi_w A_f(0) + \eta(0)}{A_t}}{CN_w(i)}} \tag{A17}$$

$$CN_{\mathrm{fd}}(i) = \left\{ C_{\mathrm{fd}}(i-1) + k_{l,\mathrm{fd}}C_l(i) + k_{\mathrm{fr},\mathrm{fd}}C_{\mathrm{fr}}(i) + \frac{(1 - F_m(i))A_d(0)}{A_t}[C_l(i) + C_{\mathrm{fr}}(i)] \right.$$

$$\left. - \frac{\xi_l A_f(0)}{A_t} \right\} \Big/ \left\{ \frac{C_{\mathrm{fd}}(i-1)}{CN_{\mathrm{fd}}(i-1)} + \frac{k_{l,\mathrm{fd}}C_l(i) + \dfrac{(1 - F_m(i))A_d(0)C_l(i) - \xi_l A_f(0)}{A_t}}{CN_{\mathrm{ls}}(i)} \right.$$

$$\left. + \frac{k_{\mathrm{fr},\mathrm{fd}}C_{\mathrm{fr}}(i) + \dfrac{(1 - F_m(i))A_d(0)C_{\mathrm{fr}}(i)}{A_t}}{CN_{\mathrm{fr}}(i)} \right\}, \tag{A18}$$

$$CN_s(i) = \frac{C_s(i-1) + \Lambda(i)[k_{\mathrm{cd},s}C_{\mathrm{cd}}(i) + k_{\mathrm{fd},s}C_{\mathrm{fd}}(i) + k_{m,s}C_m(i)]}{\dfrac{C_s(i-1)}{CN_s(i-1)} + \Lambda(i)\left[\dfrac{k_{\mathrm{cd},s}C_{\mathrm{cd}}(i)}{CN_{\mathrm{cd}}(i)} + \dfrac{k_{\mathrm{fd},s}C_{\mathrm{fd}}(i)}{CN_{\mathrm{cd}}(i)} + \dfrac{k_{m,s}C_m(i)}{CN_m}\right]}, \tag{A19}$$

$$\Delta C_w(i) = \left[f_w \mathrm{NPP}(i) - k_{w,\mathrm{cd}}C_w(i-1) - \frac{A_d(i)}{A_t}C_w(i-1) \right] \Big/ \left[1 + k_{w,\mathrm{cd}} + \frac{A_d(i)}{A_t} \right], \tag{A20}$$

$$\Delta C_{\mathrm{cr}}(i) = \left[f_{\mathrm{cr}} \mathrm{NPP}(i) - k_{\mathrm{cr},\mathrm{cd}}C_{cr}(i-1) - \frac{A_d(i)}{A_t}C_{\mathrm{cr}}(i-1) \right] \Big/ \left[1 + k_{\mathrm{cr},\mathrm{cd}} + \frac{A_d(i)}{A_t} \right], \tag{A21}$$

$$\Delta C_l(i) = \left[f_l \mathrm{NPP}(i) - k_{l,\mathrm{fmd}}C_l(i-1) - \frac{A_d(i)}{A_t}C_l(i-1) \right] \Big/ \left[1 + k_{l,\mathrm{fmd}} + \frac{A_d(i)}{A_t} \right], \tag{A22}$$

$$\Delta C_{\mathrm{fr}}(i) = \left[f_{\mathrm{fr}} \mathrm{NPP}(i) - k_{\mathrm{fr},\mathrm{fmd}}C_{\mathrm{fr}}(i-1) - \frac{A_d(i)}{A_t}C_{\mathrm{fr}}(i-1) \right] \Big/ \left[1 + k_{\mathrm{fr},\mathrm{fmd}} + \frac{A_d(i)}{A_t} \right], \tag{A23}$$

$$\Delta C_{\mathrm{cd}}(i) = \left\{ k_{w,\mathrm{cd}}C_w(i) + k_{\mathrm{cr},\mathrm{cd}}C_{\mathrm{cr}}(i) + \frac{A_d(i)}{A_t}C_w(i) + \frac{A_d(i)}{A_t}C_{\mathrm{cr}}(i) - \xi_w\frac{A_f(i)}{A_t} - \frac{\eta(i)}{A_t} \right.$$

$$\left. - 0.1(C_w(i) - \xi_w)\frac{A_f(i)}{A_t} - \xi_{\mathrm{cd}}\frac{A_f(i)}{A_t} - \Lambda(i)(k_{\mathrm{cd},a} + k_{\mathrm{cd},m} + k_{\mathrm{cd},s})C_{\mathrm{cd}}(i-1) \right\}$$

$$\Big/ \left\{ 1 + \Lambda(i)(k_{\mathrm{cd},a} + k_{\mathrm{cd},m} + k_{\mathrm{cd},s}) \right\}, \tag{A24}$$

$$\Delta C_{\text{fd}}(i) = \{(1 - F_m(i))\left[k_{l,\text{fmd}}C_l(i) + k_{\text{fr,fmd}}C_{\text{fr}}(i)\frac{A_d(i)(C_l(i) + C_{\text{fr}}(i))}{A_t}\right]$$

$$-\frac{\xi_l A_f(i)}{A_t} - \frac{\xi_{\text{fd}}A_f(i)}{A_t} - \Lambda(i)(k_{\text{fd},a} + k_{\text{fd},m} + k_{\text{fd},s})C_{\text{fd}}(i-1)\}$$

$$/\{1 + \Lambda(i)(k_{\text{fd},a} + k_{\text{fd},m} + k_{\text{fd},s})\}, \tag{A25}$$

$$\Delta C_{\text{md}}(i) = \{F_m(i)[k_{l,\text{fmd}}C_l(i) + k_{\text{fr,fmd}}C_{\text{fr}}(i) + \frac{A_d(i)}{A_t}(C_l(i) + C_{\text{fr}}(i))]$$

$$-\Lambda(i)(k_{\text{md},a} + k_{\text{md},m})C_{\text{md}}(i-1)\}/1 + \Lambda(i)(k_{\text{md},a} + k_{\text{md},m}), \tag{A26}$$

$$\Delta C_{\text{cc}}(i) = [0.1(C_w(i) - \xi_w)\frac{A_f(i)}{A_t} - k_{\text{cl},a}C_{\text{cl}}(i-1)]/[1 + k_{\text{cl},a}], \tag{A27}$$

$$\Delta C_m(i) = \{\Lambda(i)(k_{\text{cd},m}C_{\text{cd}}(i) + k_{\text{fd},m}C_{\text{fd}}(i) + k_{\text{md},m}C_{\text{md}}(i) + k_{p,m}C_p(i)) - [\Lambda(i)k_{m,a}$$
$$+ \Lambda(i-1)k_{m,s} + k_{m,p}]C_m(i-1))\}/[1 + \Lambda(i)k_{m,a} + \Lambda(i)k_{m,s} + k_{m,p}], \tag{A28}$$

$$\Delta C_s(i) = \{\Lambda(i)(k_{\text{cd},s}C_{\text{cd}}(i) + k_{\text{fd},s}C_{\text{fd}}(i) + k_{m,s}C_m(i)) - (\Lambda(i)k_{s,a} + k_{s,p})C_s(i-1)\}$$

$$/[1 + \Lambda(i)k_{s,a} + k_{s,p}], \tag{A29}$$

$$\Delta C_p(i) = \{k_{s,p}C_s(i) + k_{m,p}C_m(i) - \Lambda(i)[k_{p,a} + k_{p,m}]C_p(i)\}/[1 + \Lambda(i)(k_{p,a} + k_{p,m})].$$

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