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Multi-year carbon dioxide flux simulations for mature Canadian black spruce forests and ombrotrophic bogs using Forest-DNDC

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Ecosystem modelling is a useful tool for gaining insight and quantifying the carbon exchange between the atmosphere and terrestrial ecosystems. This study examines how well Forest-DNDC (a process-based biogeochemical model for forests/wetlands) estimates carbon dioxide (CO_2) fluxes from Canadian boreal forests and peatlands. We also evaluate the appropriateness in using Forest-DNDC to establish the baseline conditions of CO_2 fluxes before land-use change. Two mature black spruce forests and two ombrotrophic bogs were selected for comparisons between modelled and measured CO_2 fluxes. Two vegetation parameters in Forest-DNDC were optimized, and a hydrologic parameter was calibrated for the CO_2 flux simulations. The daily GPP (gross primary production) and ER (ecosystem respiration) simulations from all the study sites were in close agreement with the observations (r^2 for GPP and ER equal 0.79–0.86 and 0.86–0.87, respectively). The results of this study show that Forest-DNDC is useful in establishing baseline exchanges for boreal ecosystems prior to land-use change.

Introduction

Boreal forests and northern peatlands play an important role in the global carbon (C) cycle. Boreal forests store 295 Pg C in biomass and soils (Apps *et al*. 1993) and annually absorb ~30 g C m^{-2} (Malhi *et al*. 1999), and northern peatlands store 455 Pg C in biomass and peat (Gorham 1991) and annually take up ~20 g C m^{-2} (Gorham 1995). Without natural distur-

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bances, such as forest fires and insect outbreaks, these ecosystems act as sinks for atmospheric CO_2, but natural and anthropogenic disturbances, including possibly climate change, alter their C sink strength (e.g. Turetsky *et al*. 2002, Bond-Lamberty *et al*. 2007, Bonan 2008, Bridgham *et al*. 2008). Over the next 100 years, forest and peatland ecosystems are expected to experience significant change in their C balance as a result of warming, particularly in winter, (Stocks *et al*. 1998, Pastor *et al*. 2003) and continued pressures from land-use change as the remote higher latitudes, in particular, become progressively more economically developed.

During the last four decades, a number of process-based ecosystem models have been developed to investigate terrestrial C flux of gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) (e.g. Aber and Federer 1992, Grant *et al*. 1999, Frolking *et al*. 2002). Forest ecosystem models are used to estimate C flux from boreal forests (e.g. Kimball *et al*. 1997, Zhou *et al*. 2008), whereas wetland ecosystem models are used to estimate C flux from peatlands (e.g. Kurbatova *et al*. 2009, St-Hilaire *et al*. 2010). Typically, forest models are developed by synthesizing physiological and soil processes in upland areas (e.g. Kimball *et al*. 1997, Grant *et al*. 1999), while wetland models are developed by way of modifying forest or grassland ecosystem models to replicate the biogeochemistry of water-logged environments (e.g. Comer *et al*. 2000, Ju *et al*. 2006). When ecosystem models are adapted for peatlands, the models typically include hydrologic modules to capture water table fluctuations (Ju *et al*. 2006, Sonnentag *et al*. 2008), vegetation parameters for peatland plants (Comer *et al*. 2000), and the hydraulic and thermal soil parameters for peat (Letts *et al*. 2000). These modelling efforts are done to estimate C exchanges for the vast areas where no field measurements are available (Kimball *et al*. 2006) and/or for projections of changes in C flux under future climatic conditions (Cramer *et al*. 2001). However, in this study, we are interested in examining the effect of land-use change on C exchange due to the flooding of the boreal landscape to create reservoirs for hydroelectric power production. The examination of the land-use change effect can be complete if ecosystem models are useful in providing baseline estimates of C exchanges from boreal ecosystems. Establishing an adequate baseline is a necessary step for determining the net change in C exchange due to the reservoir creation.

Most ecosystem models focus on C simulations based on ecosystem processes that occur in the vegetation and soil. Few models use basic soil biogeochemistry such as redox chemistry. Since physiological mechanisms in vegetation dominate terrestrial C processes, many models approach C simulations by applying detailed plant functions but relatively simple soil functions (e.g. Aber and Federer 1992, Kimball *et al*. 1997). Although these models are useful for natural ecosystems, they may not be appropriate to study how C dynamics alter in response to land-cover and/or land-use changes that involve substantial changes in soil such as drainage or flooding. Flooding from the development of hydroelectric reservoirs, or drainage for logging and mining are common land-use changes that occur in the boreal biome (Bradshaw *et al*. 2009). Soil biogeochemical conditions can be dramatically altered by these land-use changes.

Forest-DNDC (Li *et al*. 2000, Miehle *et al*. 2006) contains details on the soil biogeochemistry processes that account for redox chemistry. This model captures C and nitrogen (N) dynamics of forest and wetland ecosystems by applying a daily time step and intermediate complexity of the model processes (Cui *et al*. 2005, Lamers *et al*. 2007). It has been applied widely to upland areas in forest ecosystems (e.g. Miehle *et al*. 2006, Kurbatova *et al*. 2008) as well as in forest/open wetland ecosystems (e.g. Zhang *et al*. 2002, Lamers *et al*. 2007, Kurbatova *et al*. 2009). However, Forest-DNDC has been used sparingly for boreal ecosystems. Kurbatova *et al*. (2008) conducted a simulation study of five-year CO_2 flux for two Russian spruce forest stands; Zhang *et al*. (2002) simulated two years of CO_2 and CH_4 fluxes for a Canadian fen; and Kurbatova *et al*. (2009) performed one year of CO_2 fluxes for a Russian bog using Forest-DNDC.

The Canadian boreal landscape is in high demand for hydropower developments because of the topography and sparse population. However, the hydropower developments drive the

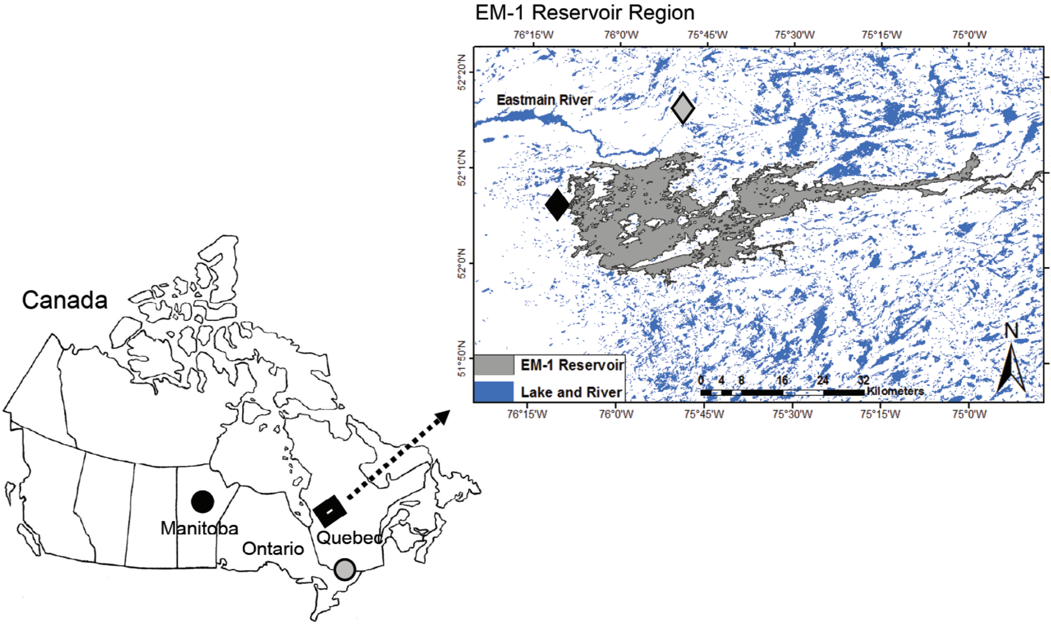

Fig. 1. Locations of the study sites: black circle — northern old black spruce (NOBS), Manitoba; gray circle — Mer Bleue peatland (MB bog), Ontario; black diamond — Eastmain-1 black spruce (EM-1 BS), Quebec; and gray diamond — EM-1 peatland (EM-1 bog), Quebec.

potential impacts on the environment, one of which is the effect on ecosystem greenhouse gas exchange. Hence, there is a need to simulate C fluxes from natural and artificially inundated landscapes to assess net changes in C storage and exchange that can be attributed to the land-use change due to flooding. Forest-DNDC has the necessary biogeochemical components to simulate the potential changes due to the inundation of living vegetation and soils. However, as a first step in our research on the effect of reservoirs on net greenhouse exchange, we need to evaluate the ability of Forest-DNDC to simulate the C flux of pristine boreal forests and peatlands. In this study, Forest-DNDC simulations of multi-year ecosystem CO_2 flux (i.e. GPP, ER, and NEP) for mature black spruce stands and ombrotrophic bogs are evaluated against field measurements. The objectives of this study were (1) to determine at what point the vegetation and soil C pools stabilize to initialize Forest-DNDC for boreal forest and peatland ecosystems; (2) to calibrate a hydrologic parameter to simulate CO_2 flux by Forest-DNDC; (3) to evaluate Forest-DNDC outputs of CO_2 flux from the boreal ecosystems against eddy covariance (EC) flux measurements of NEP and EC inferred GPP and ER; and (4) to examine sensitivity of the simulated CO_2 flux to changes in model inputs.

Material and methods

Study sites

This study used data from two boreal black spruce stands and two ombrotrophic peatlands obtained from EC flux stations (Fig. 1). The Northern Old Black Spruce (NOBS) site and the Eastern Peatland site, commonly known as Mer Bleue bog (MB bog), were part of the Fluxnet-Canada and the Canadian Carbon Program (CCP) research networks (http://fluxnet-canada.ccrp.ec.gc.ca/e_about.htm). Two recently established sites near the Eastmain-1 (EM-1) reservoir in northern Quebec (http://www.eastmain1.org/) were also used, one located in a black spruce forest (EM-1 BS) and the other on a peatland (EM-1 bog). The EM-1 reservoir was completed in spring 2006. It has a surface area of 603 km^2. Mature boreal forests, dominated by black spruce (*Picea mariana*), and peatlands, mostly bogs, are the two major land-cover types flooded by the EM-1 reservoir. They comprised respectively 30% and 18% of the total area. Young burned forests (19%), lakes and rivers (25%), and bedrock and riverbeds (8%) occupy the remaining area (Teodoru *et al*. 2011).

NOBS, located 40 km west of Thompson, Manitoba (55°53´N, 98°29´W), consists predominantly of upland forests with an interspersion of small wetland forests. Upland forests are composed of 160-year-old mature black spruce stands, and the wetlands are covered by 1- to 6-m-tall spruce and tamarack (*Larix laricina*) (Goulden and Crill 1997). The thin understory is diverse but plays a minor role at this site. Feather mosses (*Pleurozium* and *Hylocominum* spp.) and *Sphagnum* mosses cover the ground surface. Soils in the area are clayey deposits overlaid by peat of varying depths (Bond-Lamberty *et al*. 2004). Carbon dioxide flux has been measured since 1994 at NOBS (Dunn *et al*. 2007; data obtained from the ORNL DAAC [http://daac.ornl.gov/] and A. Dunn, Plant and Earth Sciences Department, Worcester State University, MA, USA).

At EM-1 BS (52°6´N, 76°11´W), vegetation consists of 84-year-old mature black spruce, in which LAI (leaf area index) is 1.7 (Lemieux 2010), and a ground cover of shrubs (e.g. *Kalmia* and *Rhododendron* spp.), feather mosses, and lichens (*Cladonia* spp.). Mineral soils in this region have an 8- to 16-cm-thick LHF (litter-humus-fermented) layer (Ullah *et al*. 2009). EM-1 BS has a 23-m EC tower that was installed in the summer of 2006 (Lemieux 2010). EC and meteorological instruments are used to measure continuous CO_2 flux and environmental variables (e.g. air temperature, precipitation, relative humidity, PAR [photosynthetically active radiation], and wind speed and direction). Details on EC and meteorological instrumentation at EM-1 BS are present in Lemieux (2010). EM-1 BS flux data are subjected to standard quality assurance procedures in accordance with the international standards of the FLUXNET community. The quality of the flux measurements were assessed using an analysis of means and standard deviations of the raw data such as wind speed and direction, air temperature, and water and CO_2 concentrations following Göckede *et al*. (2004). Gaps in measurements were filled to create continuous NEP data sets for the study period. Gaps shorter than four 30-minute periods were filled by linear interpolation, while longer gaps were filled using the standard Fluxnet-Canada algorithm (Barr *et al*. 2004). A relationship between nighttime flux and soil temperature was used to fill nighttime gaps and to compute daytime ER. A hyperbolic relationship between measured GPP and PAR (Frolking *et al*. 1998) was used to model GPP for longer daytime gaps during the growing seasons. Gaps in NEP were then filled by subtracting ER from GPP (i.e. NEP = GPP – ER) (Lemieux 2010).

MB bog is a 28-km^2 raised ombrotrophic bog near Ottawa, Ontario (45°24´N, 75°30´W). The primary vegetation communities are evergreen shrubs (*Chamaedaphne*, *Ledum*, and *Kalmia* spp.) and *Sphagnum* mosses. The secondary communities are deciduous shrubs (*Vaccinium* spp.), cottongrasses (*Eriophorum* spp.), and trees (e.g. *P. mariana* and *L. laricina*), but a few trees exist in the tower footprint. The bog surface comprises a hummock-hollow microtopography with a mean difference of 25 to 30 cm in height between hummocks and hollows (Bubier *et al*. 2003). Peat accumulation began 8500 years BP (before present) over thick silty-clay marine sediments. Peat depth ranges from 2 m at the peatland margins to > 5 m in the centre (Roulet *et al*. 2007). Flux measurements have been taken since 1998, and details of these measurements are included in Lafleur *et al*. (2003) and Roulet *et al*. (2007). The flux data were downloaded from Fluxnet-Canada and Canadian Carbon Program Data Information System (http://fluxnet-canada.ccrp.ec.gc.ca/e_DataAccess.htm).

EM-1 bog (52°17´N, 75°50´W) is a 2.2-km^2 patterned ombrotrophic bog covered by sedges (e.g. *Carex* and *Eriophorum* spp.), *Sphagnum* mosses, and sporadic evergreen shrubs. This bog has peat depths ranging from 1 to 5 m. Basal dates indicate that peat accumulation was initiated approximately 5700 years BP (van Bellen *et al*. 2011). The EM-1 bog contains a 2.75-m-tall tripod that was installed in the summer of 2008 to measure CO_2 flux and environmental variables. EC and meteorological instrumentation, flux data processing, and gap filling techniques are the same as those used for EM-1 BS.

Forest-DNDC

Model description

Forest-DNDC is a process-based biogeochemical model that simulates C and N exchanges (e.g. CO_2, CH_4, nitrous oxide (N_2O), nitric oxide (NO), and ammonia (NH_3) fluxes) in forests and wetlands from the stand-level to the regional scales (e.g. Lamers *et al*. 2007, Butterbach-Bahl *et al*. 2009, Kurbatova *et al*. 2009). For this study, version 38C of Forest-DNDC (Miehle *et al*. 2006) was adapted by modifying C modules to simulate photosynthesis by ground vegetation. Forest-DNDC was developed by an integration of the upland forest version of DNDC (PnET-N-DNDC: Li *et al*. 2000) and the wetland version of DNDC (Wetland-DNDC: Zhang *et al*. 2002). Wetland-DNDC contains hydrologic routines that can empirically estimate water table depth (WTD) if measured WTD is unavailable. The impacts of WTD on soil biogeochemistry and plant growth are also parameterized in Wetland-DNDC. Forest-DNDC simulates forest photosynthesis, respiration, and evapotranspiration mainly based on the functions developed in the PnET model (Aber and Federer 1992) and soil biogeochemistry functions adopted from the DNDC model (Li *et al*. 1992). Through this integration, Forest-DNDC has the capacity of simulating C and N cycles for both upland and wetland forest ecosystems. In Forest-DNDC, the simulated vegetation can be constructed with woody plants (i.e. overstory and understory) and ground-cover plants (e.g. herbage and moss). Gas transfers between plant, soil, and air are controlled by a number of plant, soil, and environmental inputs and parameters (Li *et al*. 2000).

Forest-DNDC has two main components. The first includes: (1) a soil climate submodel that estimates temperature, moisture, redox potential (Eh), and oxygen (O_2) concentration in the soil; (2) a forest growth submodel for growth and biomass in woody plants; and (3) a decomposition submodel that quantifies the concentration of CO_2, dissolved organic C (DOC), and NH_4^+ resulting from the mineralization of C and N. The second includes soil modules for nitrification, denitrification, and CH_4 production and oxidation to estimate the concentrations of NO, N_2O, CH_4, and NH_3 in the soil. The partitioning of processes and exchanges between the first and second components are controlled by a conceptualization of the redox state by an 'anaerobic balloon' whose size is determined by Eh and O_2 concentration of the soil (Miehle *et al*. 2006). More information on the model structure and functions of Forest-DNDC is provided in Li *et al*. (2000), Butterbach-Bahl *et al*. (2004), and Cui *et al*. (2005).

Ground vegetation functions

In Forest-DNDC, photosynthesis by ground vegetation is estimated using a light-use-efficiency approach in which photosynthesis is controlled by light and air temperature. However, this approach lacks representation of the soil moisture effects on ground vegetation photosynthesis. This is particularly important for mosses that lack a vascular system and roots. As an enhanced photosynthesis module, ground vegetation functions were incorporated based on a description into the SPAM model (Frolking *et al*. 1996) as follows:

$$\begin{aligned}\mathrm{PSN}_{\mathrm{Ground}} = {} & B_{\mathrm{Ground}} \times A_{\mathrm{Max}} \times F_{\mathrm{Temp}} \times F_{\mathrm{Water}} \\ & \times F_{\mathrm{GDD}} \times F_{\mathrm{Light}} \times \mathrm{DL}\end{aligned} \quad (1)$$

where $\mathrm{PSN}_{\mathrm{Ground}}$ is the daily gross photosynthesis in ground vegetation (g C m^{-2} d^{-1}); B_{Ground} is the biomass of ground vegetation (g C m^{-2}); A_{Max} is the maximum net photosynthetic rate per moss biomass per hour (mg CO_2 g^{-1} h^{-1}); F_{Temp}, F_{Water}, F_{GDD}, and F_{Light}, respectively, indicate scale factors to quantify the effects of air temperature, soil moisture, growing degree days (GDD), and light on the photosynthetic process; and DL is the day length per day (h d^{-1}). The functions for F_{Temp}, F_{GDD}, and F_{Light} are the same as in previous studies (Frolking *et al*. 1996, Zhang *et al*. 2002), while the function of F_{Water} is a newly developed function adapted from the relationship between water potential in the surface soil layer and photosynthetic activity in *Sphagnum* moss (Hájek and Beckett 2008):

$$F_{\mathrm{Water}} = 0, \text{ if } \mathrm{WFPS} \leq \mathrm{WFPS}_{\mathrm{Wilting}} \quad (2)$$

$$F_{\text{Water}} = 0.1 + 0.9(\text{WFPS} - \text{WFPS}_{\text{Wilting}})/(\text{WFPS}_{\text{Saturated}} - \text{WFPS}_{\text{Wilting}}), \text{ if } \text{WFPS}_{\text{Wilting}} < \text{WFPS} \leq \text{WFPS}_{\text{Adequate}} \quad (3)$$

$$F_{\text{Water}} = 1, \text{ if } \text{WFPS}_{\text{Adequate}} < \text{WFPS} \leq \text{WFPS}_{\text{Saturated}} \quad (4)$$

where WFPS (water-filled pore space: 0–1) indicates soil moisture content in the first layer of organic soil (forests: 0–2.1 cm; peatlands: 0–12 cm). Values for WFPS in the model setting are $\text{WFPS}_{\text{Wilting}} = 0.2$ (Hájek and Beckett 2008); $\text{WFPS}_{\text{Adequate}} = 0.78$ (Hájek and Beckett 2008); and $\text{WFPS}_{\text{Saturated}} = 0.98$ (default in Forest-DNDC).

Simulation of CO_2 fluxes

Forest-DNDC simulates daily GPP and ER, and daily NEP is calculated as the difference between the two (i.e. NEP = GPP – ER). Annual CO_2 flux of GPP, ER, and NEP is the accumulation of daily CO_2 fluxes over a year. The relative error of NEP is larger than that found in GPP and ER since the magnitude of NEP is generally much smaller than that of GPP or ER, and NEP accumulates the errors in each of GPP and ER. As the NEP value gets closer to 0, zero net exchange, the relative errors in NEP become infinite.

Model database

Input variables

Forest-DNDC requires climate inputs of daily maximum and minimum air temperature (°C) and precipitation (cm). Measurements from the study sites provided most inputs, and the missing inputs were derived from linear regressions between the tower measurements and the nearest weather station of the Meteorological Service of Canada (MSC) or Hydro-Québec for periods of the co-incident measurements. Wet N deposition data were obtained from Canadian National Atmospheric Chemistry (NATChem) monitoring stations closest to each of NOBS, MB bog, and the EM-1 reservoir. We used measurements of water table for the entire study period for MB bog (Moore *et al*. 2011), while the Forest-DNDC empirical functions were used to estimate water tables for EM-1 bog since the measured water table data were available only for part of the study years (Pelletier *et al*. 2011). Lastly, forest and soil types, ground vegetation biomass, and soil properties (e.g. pH and thickness of organic and mineral soils) were determined by way of field observations at the sites themselves or through the default values in Forest-DNDC (Table 1).

Vegetation and soil parameters

Forest-DNDC sets woody vegetation parameters for the overstory and understory as well as soil parameters for the organic and mineral soils based on woody vegetation species, soil type, and site information such as latitude and wet N deposition. For the sites used in this study, vegetation layers were simplified into one of the two dominant woody vegetation types (trees at forest sites and shrubs at peatland sites) and ground vegetation (mosses at both forest and peatland sites). Vegetation parameters were set as model defaults, or based on field measurements or the literature (Appendix). Defaults of Forest-DNDC for spruce (forest sites) and vascular plant types (peatland sites) were used first. However, if field measurements or literature values were available and more appropriate, they were used. Model defaults were used for all soil parameters in the organic and mineral layers (e.g. bulk density, clay content, and porosity).

Spin-up runs with parameter optimization

The initial woody vegetation C mass in leaf, wood, and root as well as soil organic C (SOC) in the organic and mineral layers were set after spin-up runs were complete. Spin-up runs are repetitive simulations using the same inputs and parameters over many years to determine when a steady state in the C pools is reached. Forest-DNDC does not model individual trees but models the biomass and C stored in trees on a unit area basis. The simulated C storage values through the spin-up runs are for NOBS, ~56 t C of above-ground biomass from ~6000 trees in a hectare area (Gower *et al*. 1997), and for EM-1 BS, ~35 t C of the biomass from ~5000 trees in a hectare area (Lemieux 2010). We defined the steady-state of all the sites when there was the lowest rate of change in the living woody biomass pool in Forest-DNDC.

A total of 200 years of spin-up simulations were carried out for the forest sites by applying the averaged measured climate from the tower sites, and the same years of simulations were conducted for peatland sites by applying the averaged climate and WTD during the study period. Model inputs and woody vegetation parameters used in the tests are listed in Table 1 and Appendix, respectively. The two woody vegetation parameters, AmaxFrac (daily maximum photosynthetic rate as a fraction of early morning instantaneous rate) and FolNCon (foliage N concentration by weight), were optimized for EM-1 BS. The value range of AmaxFrac (0.36–0.93: Fan *et al*. 1995) and FolNCon (0.5%–1.1%: Watt and Heinselman 1965) is well-documented for black spruce forests.

Initial C inputs for spin-up runs were one-year-old biomass in woody vegetation, set at the Forest-DNDC default, and the measured SOC from the study sites (Table 2). The year of stabilization (the lowest rate of change, at the inflection point, in woody biomass after the peak biomass) indicates the stage of the maximum growth of biomass and the smallest vegetation mortality. Stable woody vegetation and soil values from these tests were then used as initial

Table 1. Description of model inputs used in this study.

Variable (unit)	Value/setting			
	NOBS	EM-1 BS	MB bog	EM-1 bog
Site				
Lat. (°W)	55.88	52.1	45.4	52.29
Wet N deposition (ppm)	0.77[a]	0.59[b]	2.12[c]	0.59[b]
Climate (growing season; non-growing season)[d]				
Daily maximum temperature (°C)	15.1; –8.1	15.1; –6.5	21.7; 4.1	14.9; –7.9
Daily minimum temperature (°C)	4.3; –17.7	6.4; –15.1	8.5; –8.3	3.7; –19.0
Daily precipitation (cm)	0.15; 0.02	0.32; 0.05	0.31; 0.23	0.32; 0.05
Hydrology[e]				
Water table depth (cm)	NA	NA	42; 30	6; 12
Vegetation				
Type of woody vegetation	Black spruce	Black spruce	Evergreen shrub	Evergreen shrub
Ground vegetation biomass (g C m^{-2})	97[f]	111[g]	76[h]	46[i]
Soil				
Type of organic soil	Mor[j]	Mor[j]	Mor[j]	Mor[j]
Type of mineral soil	Clay[f]	Sandy loam[k]	Silty-clay[l]	Clay[m]
Thickness in organic soil (m)	0.042[n]	0.042[n]	3.0[o]	2.7[p]
Thickness in mineral soil (m)	0.5[n]	0.5[n]	0.02[n]	0.021[n]
Number of organic soil layer	2[n]	2[n]	25[n]	22[n]
Number of mineral soil layer	23[n]	23[n]	1[n]	1[n]
pH in organic soil	5.9[r]	4.3[k]	3.9[s]	3.8[p]
pH in mineral soil	6.8[r]	5.4[k]	6.0[t]	6.0[t]

[a,b,c] Database of National Atmospheric Chemistry (NAtChem), Environmental Canada: [a] mean of the period from 1984 to 1997 at the station of Island Lake, Manitoba (53°54´N, 94°42´W); [b] mean of the period from 2004 to 2005 at the station of LG4, Quebec (53°48´N, 73°42´W); and [c] mean of the period from 1984 to 2004 at the station of Chalk River, Ontario (46°0´N, 77°24´W). [d] Mean of growing season (May–October) and non-growing season (November–April): from 1995 to 2006 in NOBS; from 1999 to 2006 in MB bog; and from 2006 to 2009 in EM-1 BS and bog. [e] Averaged water table depth in growing season (May–October) and non-growing season (November–April): from 1998 to 2006 in MB bog and from 2008 to 2009 in EM-1 bog. [f] Gower *et al.* 1997. [g] Lemieux 2010. [h] Moore *et al.* 2002. [i] Pelletier *et al.* 2011. [j] Prescott *et al.* 2000. [k] J. Banville unpubl. data. [l] Lafleur *et al.* 2001. [m] Protz *et al.* 1988. [n] Default in Forest-DNDC. [o] Frolking *et al.* 2002. [p] S. van Bellen unpubl. data. [r] Savage *et al.* 1997. [s] Bubier *et al.* 2003. [t] Vitt and Wieder 2006. NA: not applicable.

conditions for the subsequent simulations during the study periods (Table 2).

Calibration of water table depth

The simple hydrologic submodel within Forest-DNDC was applied to EM-1 bog because WTD was measured only for a short period of time (May 2008 to November 2009), but the measured WTD was used for the MB bog simulations. The hydrologic submodel that estimates daily WTD needs daily climate inputs and six hydrologic parameters: initial WTD, the surface inflow fraction of precipitation, the rates of surface outflow and ground outflow, and the lowest WTD where surface outflow and ground outflow ceases. Of these six parameters, three were obtained from field measurements in EM-1 bog (initial WTD: –11 cm; the lowest WTD where surface outflow ceases: 0 cm; and the lowest WTD where ground outflow ceases: –25 cm); two were taken from an application of the wetland version of Forest-DNDC applied to a peatland in western Canada (the surface inflow fraction of precipitation: 1; and the rate of ground inflow: 0.006) (Zhang *et*

Table 2. Description of model inputs for woody vegetation and soil that were defined by spin-up simulations. Start indicates values used in spin-up simulations, and stabilization indicates steady-state values after spin-up simulations were completed.

Variable (unit)	Description	NOBS		EM-1 BS	
		Start	Stabilization	Start	Stabilization
Forest site					
Year (yr)	Age	1	157	1	120
Leaf (g C m^{-2})	Initial leaf biomass	31	381	40	383
Wood (g C m^{-2})	Initial woody biomass	19	5904	22	3078
FineRoot (g C m^{-2})	Initial fine root biomass	31	206	40	212
MaxLeaf (g C m^{-2})	Maximum leaf biomass	41	423	53	410
MinLeaf (g C m^{-2})	Minimum leaf biomass	31	381	40	383
BudC (g C m^{-2})	Initial available C stored in bud	10	67	13	42
WoodC (g C m^{-2})	Initial available C stored in woody biomass	26	33	33	13
PlantC (g C m^{-2})	Initial available C stored in plant	36	101	47	55
Organic SOC (g C m^{-2})	Soil organic carbon (SOC) in organic soil	9900[a]	2339	9011[b]	2468
Mineral SOC (g C m^{-2})	SOC in mineral soil	7300[a]	5888	10806[b]	10708
		MB bog		EM-1 bog	
		Start	Stabilization	Start	Stabilization
Peatland site					
Year (yr)	Age	1	117	1	93
Leaf (g C m^{-2})	Initial leaf biomass	18	197	10	120
Wood (g C m^{-2})	Initial woody biomass	39	1127	25	966
FineRoot (g C m^{-2})	Initial fine root biomass	18	107	10	653
MaxLeaf (g C m^{-2})	Maximum leaf biomass	37	218	21	143
MinLeaf (g C m^{-2})	Minimum leaf biomass	18	197	10	120
BudC (g C m^{-2})	Initial available C stored in bud	18	34	10	36
WoodC (g C m^{-2})	Initial available C stored in woody biomass	37	4	21	8
PlantC (g C m^{-2})	Initial available C stored in plant	55	38	31	43
Organic SOC (g C m^{-2})	SOC in organic soil	72000[c]	73758	110000[d]	112822
Mineral SOC (g C m^{-2})	SOC in mineral soil	620[e]	862	625[e]	845

[a] Bergeron *et al.* 2007. [b] J. Banville unpubl. data. [c] Frolking *et al.* 2002. [d] van Bellen *et al.* 2011. [e] Estimated using average SOC concentration in mineral soils: 0.031 g C g^{-1} (Moore and Turunen 2004).

al. 2002); and the rate of surface outflow was calibrated for this study.

Model evaluation

The goodness of fit between measured and modelled daily CO_2 flux was assessed using the RMSE (root mean square error, g C m^{-2} d^{-1}) and d (index of agreement, ranging from 0 to 1). To derive d, the systematic RMSE (RMSEs: errors resulting from model prediction) and unsystematic RMSE (RMSEu: errors related to measurements) were needed, and the RMSE and d were calculated using Eqs. 5 to 9 (Willmott *et al*. 1985):

$$\mathrm{RMSE} = \sqrt{\left[\frac{1}{n}\sum_{i=1}^{n}\left(P_i - M_i\right)^2\right]} \tag{5}$$

$$\mathrm{RMSEs} = \sqrt{\left[\frac{1}{n}\sum_{i=1}^{n}\left(P_i^* - M_i\right)^2\right]} \tag{6}$$

$$\mathrm{RMSEu} = \sqrt{\left[\frac{1}{n}\sum_{i=1}^{n}\left(M_i^* - M_i\right)^2\right]} \tag{7}$$

$$\mathrm{RMSE}^2 = \mathrm{RMSEs}^2 + \mathrm{RMSEu}^2 \tag{8}$$

$$d = 1 - \frac{n\mathrm{RMSE}^2}{\sum_{i=1}^{n}\left(\left|P_i'\right| - \left|O_i\right|\right)^2} \tag{9}$$

where n is the number of values, P_i is the model-predicted ith value, M_i is the measured ith value, $P_i* = a + bM_i$ (a and b are the parameters from the least-squared linear regression between P and M), $P_i' = P_i$ – (mean M), and $M_i' = M_i$ – (mean M).

Annual CO_2 flux was evaluated by calculating the average absolute difference (g C m^{-2} yr^{-1}) and average percentage difference (%) between measured and simulated annual GPP, ER, and NEP. Percentage errors in modelling (E_{Model}, %) and measurement (E_{Measured}, %) for annual CO_2 flux were determined using the potential uncertainty in EC measurements (i.e. ±25% of the measured value: Griffis *et al*. 2003) and the three daily flux RMSE (RMSEs, RMSEu, and RMSE: mainly related to errors in measurement, modelling, and the total for daily flux, respectively). The uncertainty in EC measurements represented E_{Measured}. The daily RMSEs was estimated using the daily RMSE and RMSEu (25% of mean measured daily flux) and a relationship among the three RMSE (Eq. 8), and then E_{Model} was determined as percentage of RMSEs against mean modelled daily flux.

Better agreement between model predictions and measurements was indicated by lower RMSE, lower absolute and percentage difference, and higher d. Especially, $d > 0.8$ were accepted as good estimates by models (Legates and McCabe 1999).

Sensitivity analysis

For both NOBS and MB bog, sensitivity analysis was carried out to test GPP, ER, and NEP variations by applying a 20% increase and decrease to the required inputs except for type and age of woody vegetation and thickness and number of organic and mineral soils (Tables 1 and 2: 22 variables). Sensitivity was evaluated by calculating the magnitude of altered annual CO_2 flux between simulations using the fixed values in Tables 1 and 2 (i.e. reference simulation) and the altered input (i.e. sensitivity simulation).

Results

Spin-up runs and calibration

Stabilization of vegetation and soil C pools

The age when woody vegetation reached stabilization for the forest sites was reasonable compared with stand age from field measurements (Fig. 2). NOBS stabilized after 157 years, and the actual stand age was 160 years (Gower *et al*. 1997). EM-1 BS stabilized after 120 years, and the actual stand age was 84 years (Lemieux 2010).

Small differences existed between the measured above-ground tree biomass (the sum of woody and leaf biomass) (5624 g C m^{-2}: 396 g C m^{-2} in leaf; 5228 g C m^{-2} in wood, Gower *et al*. 1997) and the biomass derived from the spin-up simulations (6284 g C m^{-2}: 380 g C m^{-2} in leaf; 5904 g C m^{-2} in wood) for NOBS (Fig. 2). However, the spin-up simulations produced

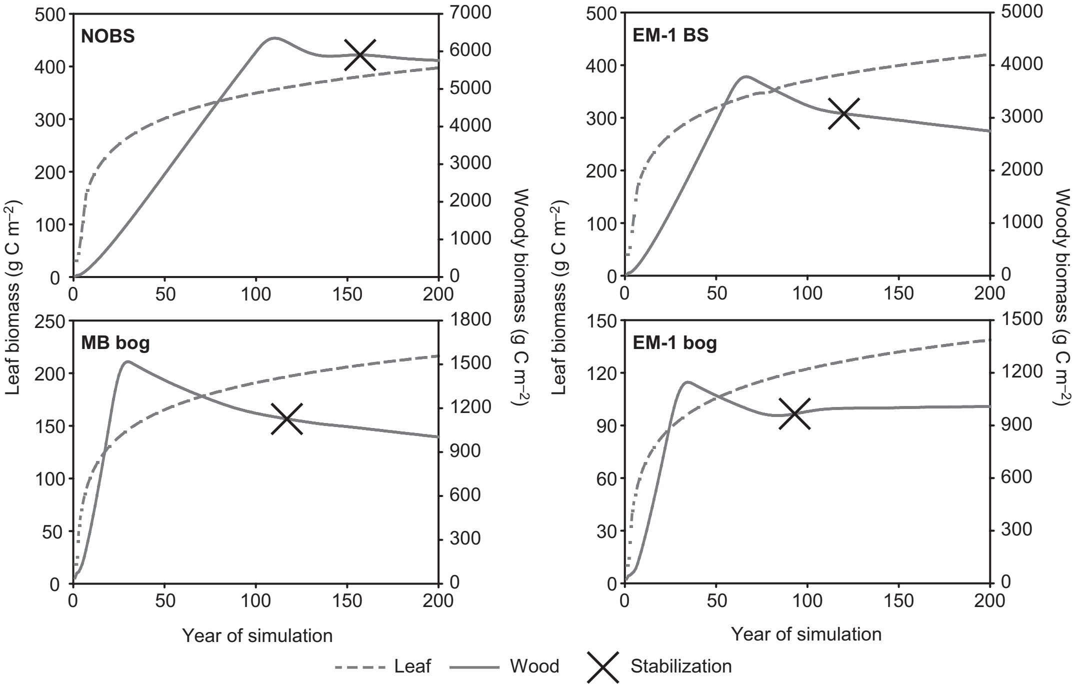

Fig. 2. Leaf biomass (g C m^{-2}) and woody biomass (g C m^{-2}) of woody vegetation on the first day of the year, determined during the 200 year spin-up simulations for the forest sites (NOBS and EM-1 BS) and peatland sites (MB bog and EM-1 bog). The time when the amount of biomass stabilizes is indicated.

5995 g C m^{-2} (395 g C m^{-2} in leaf; 5600 g C m^{-2} in wood) for EM-1 BS, which was greater than that from the field measurements (3519 g C m^{-2}: 310 g C m^{-2} in leaf; 3209 g C m^{-2} in wood; Lemieux 2010). AmaxFrac and FolNCon were optimized within the range of values reported in the literature to reduce this difference between measured and simulated equilibrium biomass values. AmaxFrac at 0.74 and FolNCon at 0.6% gave acceptable results: observation of 3519 g C m^{-2} versus simulation of 3461 g C m^{-2} (383 g C m^{-2} in leaf, 3078 g C m^{-2} in wood) (Fig. 2).

The same woody vegetation parameter values (Appendix) were used for modelling at the peatland sites without parameter optimization. A large difference appeared when the measured shrub biomass and spin-up simulated woody biomass were compared: the measured shrub biomass was 149 g C m^{-2} (73 g C m^{-2} in leaf; 76 g C m^{-2} in stem, Moore *et al*. 2002) at MB bog and 21 g C m^{-2} (10 g C m^{-2} in leaf; 11 g C m^{-2} in stem, Pelletier *et al*. 2011) at EM-1 bog. The biomass from the spin-up runs was 1324 g C m^{-2} (197 g C m^{-2} in leaf; 1127 g C m^{-2} in wood) in MB bog and 1 086 g C m^{-2} (120 g C m^{-2} in leaf; 966 g C m^{-2} in wood) in EM-1 bog (Fig. 2). There is no tree biomass data for MB bog or EM-1 bog, since there was a sparse tree cover. The use of shrub biomass measurements underestimated the true biomass in woody vegetation from both of the study peatlands. Even though the peatlands are categorized as open bogs, there is tree biomass (e.g. small coniferous trees) especially in the margins of the peatlands. For comparison, an open bog in Ontario showed that trees comprised two times more biomass than what was measured from shrubs (1179 g C m^{-2} in trees and 500 g C m^{-2} in shrubs: Dyck and Shay 1999). Thus, while we could not directly compare the woody biomass, the values of the biomass produced by Forest-DNDC were within the range reported in the literature.

Our biomass setting from the spin-up simulations with no parameter optimization led to the reasonable C fluxes for the study peatlands. If the spin-up biomass were significantly overestimated, we would expect unreasonably high simulated GPP and ER. However, for both MB

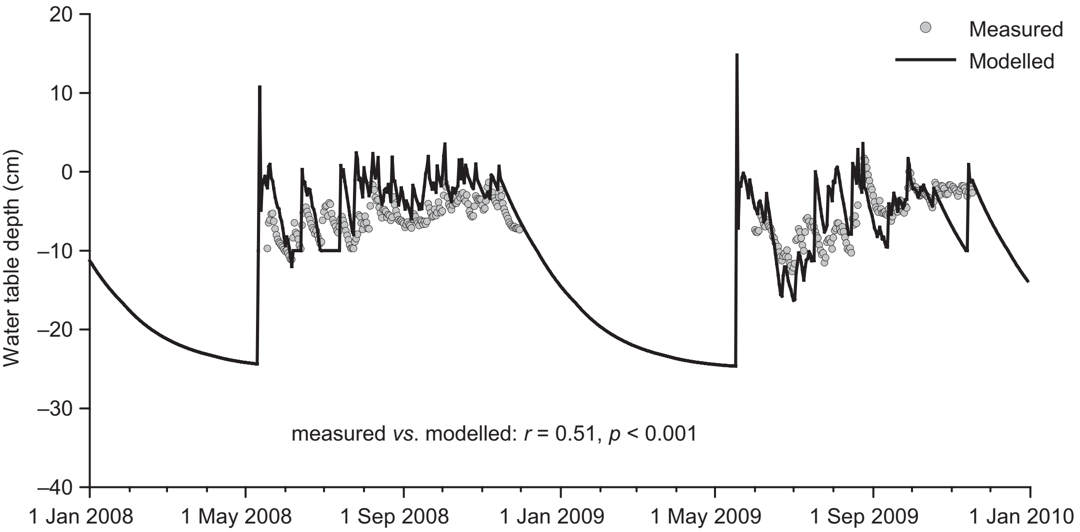

Fig. 3. Comparison between measured and modelled daily water table depth (WTD, cm) for EM-1 bog. Modelled WTD is from the calibration of a hydrologic parameter (the intensity factor for surface outflow), including the least errors against the observations.

bog and EM-1 bog, the ranges of simulated GPP and ER were similar to the measured GPP and ER (*see* 'Peatland sites' below).

Calibration of a hydrologic parameter

The rate of surface outflow was calibrated to provide the best fit between measured and simulated WTD (Fig. 3): a value of 1.3 was established.

Daily simulation of CO_2 fluxes

Forest sites

Fluctuations in modelled CO_2 flux for NOBS corresponded well with the measurements (Fig. 4A), but simulated GPP and NEP were positive earlier than the observations for years with the earliest growing seasons. Measured fluxes in GPP, ER, and NEP often exceeded the simulated fluxes during the growing seasons. GPP and ER had a low RMSE and a high *d* relative to those for NEP (Fig. 4B). Forest-DNDC slightly underestimated GPP and ER, which resulted in either a slight underestimation of negative NEP (i.e. ER > GPP) or a slight overestimation of positive NEP (i.e. GPP > ER).

Annual patterns in measured and simulated CO_2 fluxes were similar for EM-1 BS. Simulated GPP and ER during the growing seasons were higher than the observations (Fig. 5A), and similar to NOBS, the RMSE and *d* were reasonable for GPP and ER, but NEP was simulated much more poorly (Fig. 5B). Although one-to-one comparisons showed strong relationships ($p < 0.001$) between measured and modelled fluxes, whereas modelled GPP and ER were overestimated and modelled NEP was consistently underestimated.

Peatland sites

Seasonal changes in simulated CO_2 flux were consistent with measured seasonal changes for MB bog (Fig. 6A). Simulated GPP and ER were in good agreement with observations, but discrepancies in GPP were greater during the summer and autumn months of 1999 and between 2004 and 2006. These translated into errors in NEP: simulated NEP < measured NEP for these periods. Simulated GPP was slightly underestimated, but ER was agreed with measurements (Fig. 6B), leading to a small underestimation of NEP.

Forest-DNDC simulated CO_2 fluctuation patterns well for the limited 1.5 years of observa-

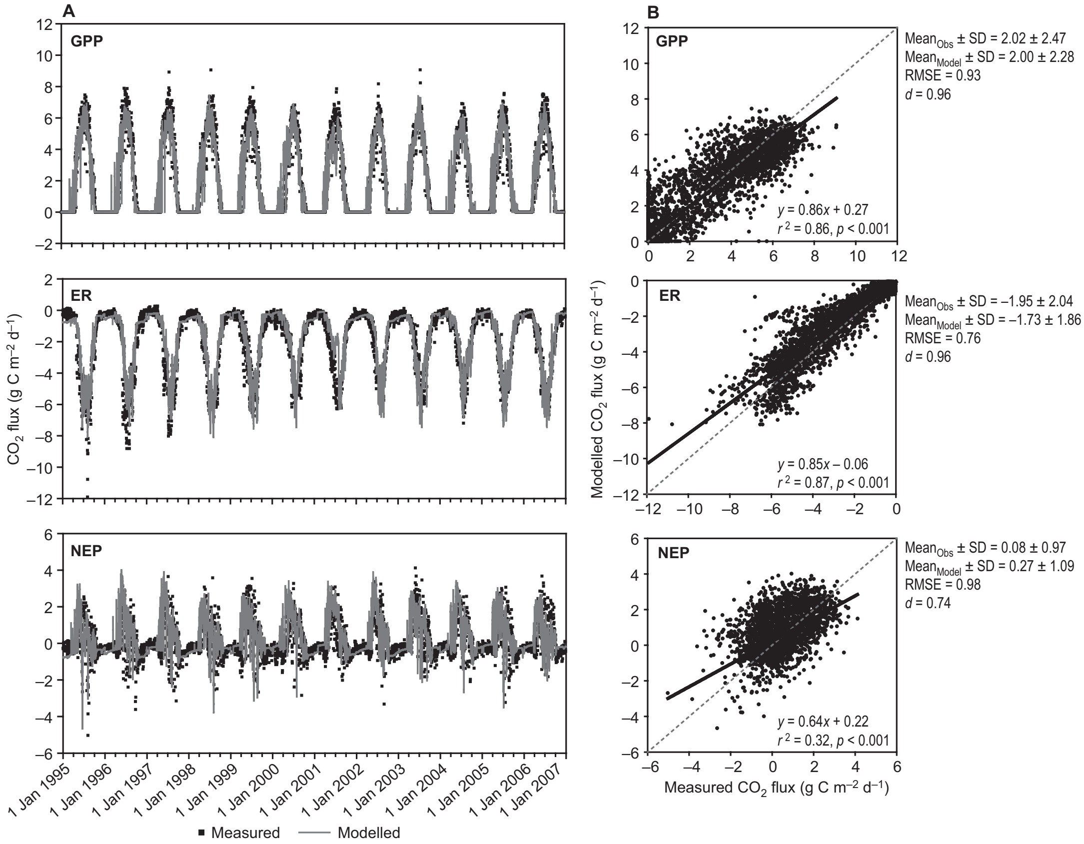

Fig. 4. (**A**) Measured and modelled daily CO$_2$ fluxes (GPP, ER, and NEP) (g C m^{-2} d^{-1}), and (**B**) relations between measured and modelled fluxes for NOBS (n = 4380). The sign of CO$_2$ flux represents the direction of the flux: a positive flux is from the atmosphere to ecosystems, while a negative flux is the opposite direction. 'Obs' and 'Model' refer to measured and simulated fluxes, respectively. Thick black lines in **B** are linear regressions between the two variables, and dashed grey lines are 1:1 line.

tions at EM-1 bog (Fig. 7A). A discrepancy in GPP was evident for the earlier growing season. ER had its greatest discrepancy during the mid-growing seasons, which translated into the mid-growing season NEP discrepancy. GPP and ER were slightly underestimated throughout the study period (Fig. 7B), leading to an underestimation of NEP.

Annual simulation of CO$_2$ fluxes

Overal, as compared with the measurements, simulations from NOBS systematically underestimated annual ER and overestimated annual GPP and NEP (Fig. 8a–c). A strong correlation in the year-to-year change in GPP and ER appeared, but the relationship for NEP was much weaker. Averages in absolute differences (percentage difference in parenthesis) during the study period resulted in reasonable levels of 40 g C m^{-2} yr^{-1} (6%) for GPP, 86 g C m^{-2} yr^{-1} (12%) for ER, and 95 g C m^{-2} yr^{-1} (720%) for NEP. EM-1 BS simulations overestimated annual GPP and ER, but simulated NEP was quite similar to the measured flux (Fig. 8a–c). Means of absolute differences (percentage difference in parenthesis) during the study period were 116 g C m^{-2} yr^{-1} (22%) for GPP, 115 g C m^{-2} yr^{-1} (25%) for ER, and 16 g C m^{-2} yr^{-1} (24%) for NEP.

Simulated annual GPP and NEP were greater than measurements for MB bog, but simulated annual ER was generally underestimated (Fig. 8d–f). Means of absolute differences (per-

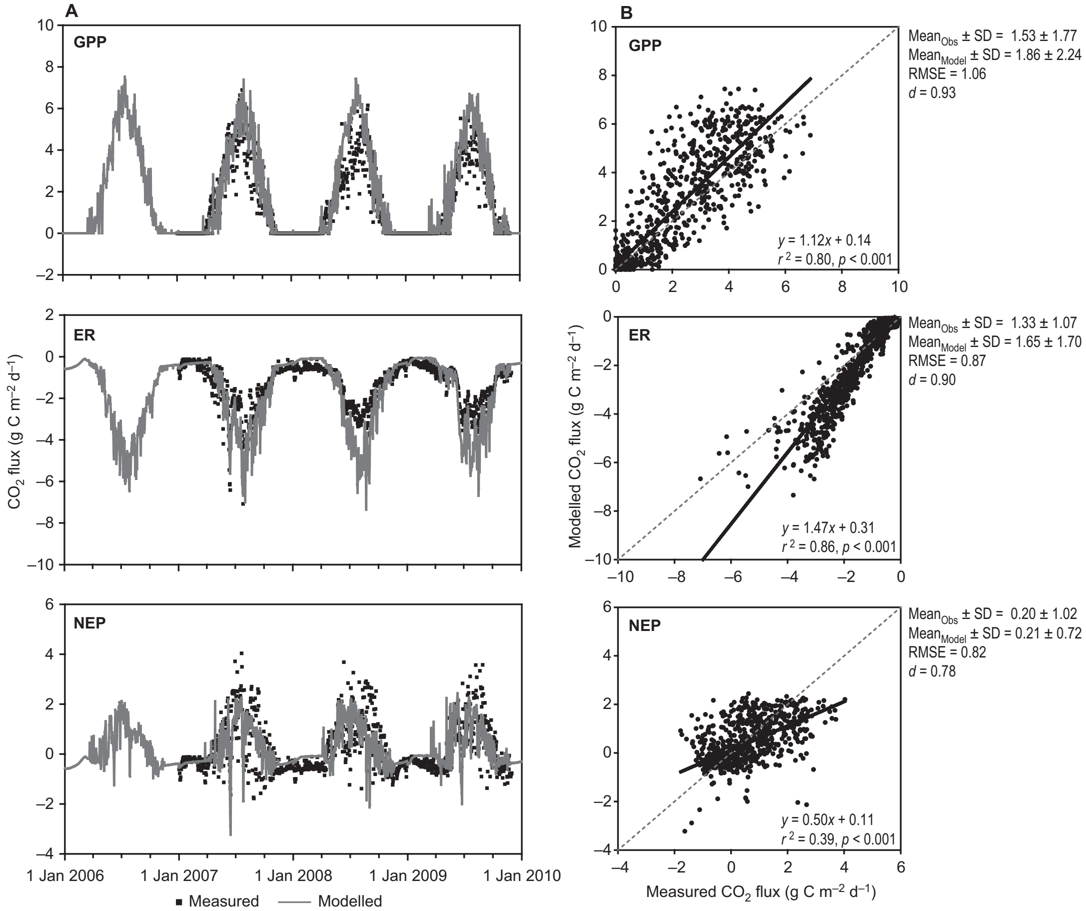

Fig. 5. (**A**) Measured and modelled daily CO_2 flux patterns (GPP, ER, and NEP) (g C m^{-2} d^{-1}) and (**B**) relations between measured and modelled fluxes for EM-1 BS (*n* = 1 064). For explanations *see* the caption to Fig. 4.

centage difference in parenthesis) were small: 94 g C m^{-2} yr^{-1} (18%) for GPP, 58 g C m^{-2} yr^{-1} (10%) for ER, and 66 g C m^{-2} yr^{-1} (614%) for NEP. Simulations generated reasonable predictions for EM-1 bog with only a small range of discrepancy (Fig. 8d–f) with averaged absolute differences (percentage difference in parenthesis) of 39 g C m^{-2} yr^{-1} (15%) for GPP, 16 g C m^{-2} yr^{-1} (8%) for ER, and 38 g C m^{-2} yr^{-1} (5%) for NEP.

Sensitivity analysis

High sensitivity (arbitrarily defined as ≥ 10% response in either GPP or ER) was measured for 5 of 22 inputs for the Forest-DNDC simulations (Table 3). NEP sensitivity was greater than GPP and ER sensitivity. This is due to NEP being calculated as the difference between simulated GPP and ER as well as being a factor of 1.5 to 58 times smaller than either GPP or ER. There was high sensitivity to the climate inputs, and only two soil inputs produced a strong response to C flux. Daily maximum and minimum temperatures and the types of organic and mineral soil produced higher sensitivities in the forest simulations, while the same sensitivities occurred for peatlands with the exception of the soil variables. It is interesting to note that the particular type of organic soil provided high sensitivity in ER for forest simulations because this parameter influences the quality of forest organic soil, which in turn largely affects soil respiration. Although the changed organic soil type (mull) does not exist in the study forests and peatlands, this sensitivity

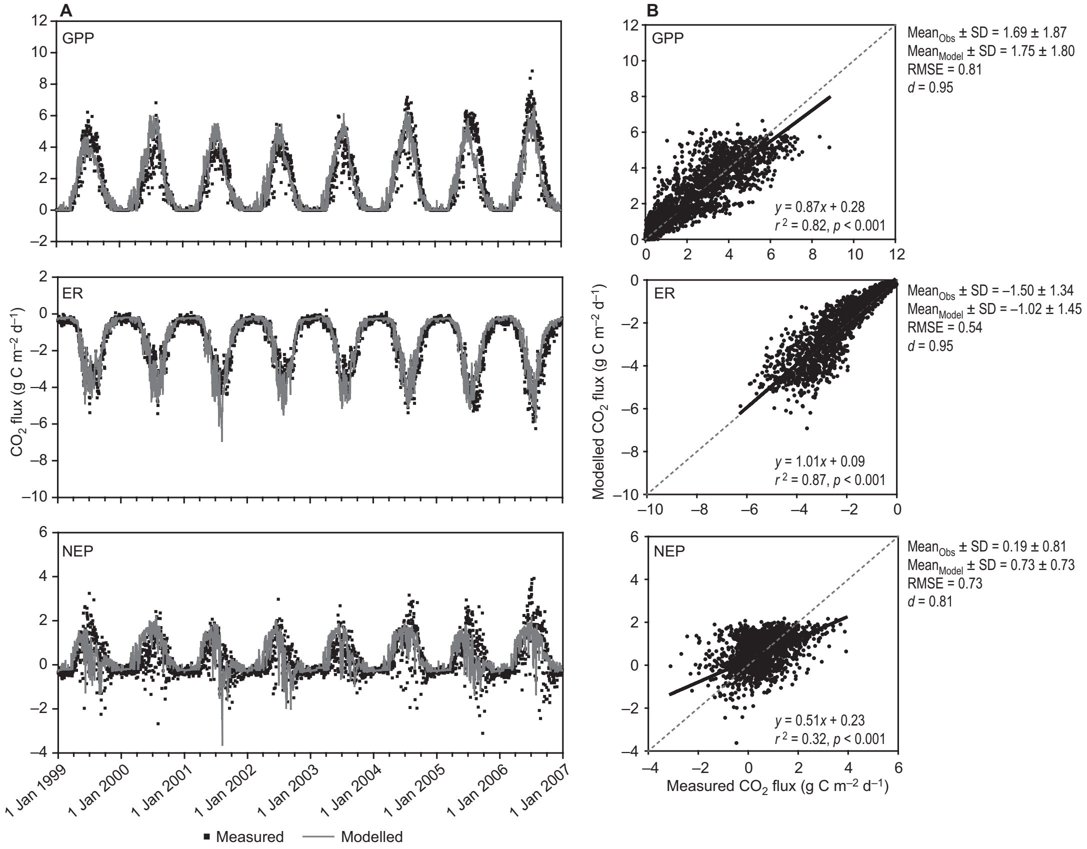

Fig. 6. (**A**) Measured and modelled daily CO$_2$ flux patterns (GPP, ER, and NEP) (g C m^{-2} d^{-1}) and (**B**) relations between measured and modelled fluxes for MB bog (n = 2 920). For explanations *see* the caption to Fig. 4.

analysis by the extreme change among the three organic soil types in Forest-DNDC (mor to mull) indicates the importance of setting the soil type for C flux simulations.

Discussion

In this study, Forest-DNDC, as is the case with all models, does not reproduce field measurements exactly, but our results show that Forest-DNDC provides reasonable estimates of daily and annual CO$_2$ fluxs (Figs. 4–7 and 8, respectively) from Canadian black spruce forest and peatland ecosystems. 'Reasonable' is a relative term, so its meaning needs to be assessed in terms of what Forest-DNDC is used to estimate. In this study, we looked for a model that could estimate CO$_2$ fluxes for the main boreal ecosystems where reservoirs are created. By flooding the landscape, we expect changes of several hundred g C m^{-2} yr^{-1} in GPP and ER. Within this context, the uncertainties based on our study are 27%–35% by combining GPP and ER errors (r^2 = 0.79–0.86 for GPP; r^2 = 0.86–0.87 for ER: Figs. 4–7) of the expected change. The degree of discrepancy (expressed by RMSE and d) for NEP was much higher than that for GPP and ER, but NEP was relatively small at all sites: ~100 g C m^{-2} yr^{-1} or less. Therefore, a combination of errors for GPP and ER always yields relatively large errors in NEP despite a reasonable estimate of GPP and/or ER.

Modelling reliability and utility were additionally evaluated based on comparisons between our results and two other studies. Recent studies of C flux modelling were carried out at NOBS and MB bog during the same periods as in this study. Grant *et al.* (2008) published NOBS simulations from 2004 to 2006 using a forest model,

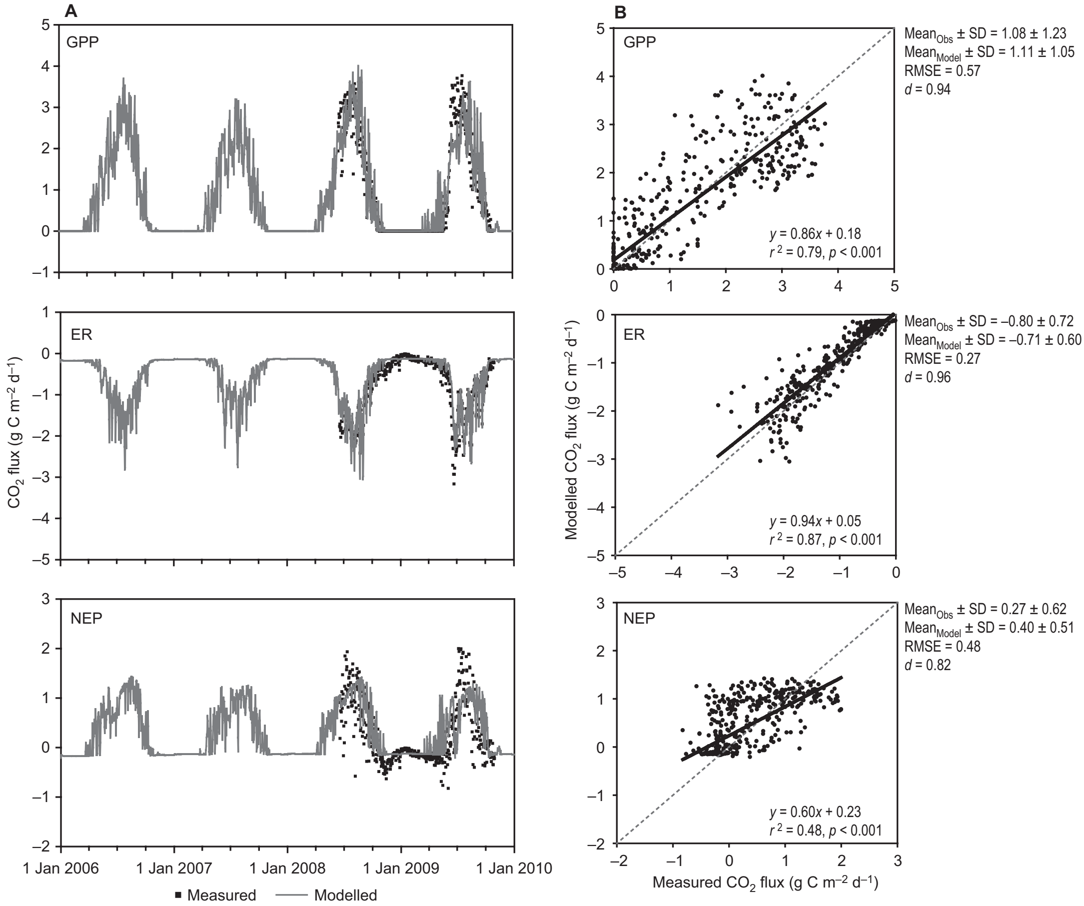

Fig. 7. (**A**) Measured and modelled daily CO_2 flux patterns (GPP, ER, and NEP) (g C m^{-2} d^{-1}) and (**B**) relations between measured and modelled fluxes for EM-1 bog ($n = 498$). For explanations *see* the caption to Fig. 4.

ecosys, and St-Hilaire *et al*. (2010) carried out MB bog simulations from 1999 to 2006 using the McGill Wetland Model (MWM). We recognize that a model to model comparison does not provide any evidence of the performance of a model, but it allows one to determine if the models have similar or markedly different abilities to mimic reality. All simulations indicate that NOBS and MB bog sequester C and that Forest-DNDC simulations produce a similar range of C fluxes as estimated by ecosys and MWM (Fig. 9). Both ecosys and MWM are detailed models and have hourly time step, requiring much more and less readily available input data than Forest-DNDC. In this respect, Forest-DNDC has an advantage in simulating C flux according to the comparison of the annual exchanges where Forest-DNDC appears to perform equally well as ecosys and MWM do especially at least in Canada, where most reservoirs are built in very remote locations.

Sensitivity analysis provides an understanding of model behaviour in response to changes in model inputs. Similar results in NOBS and MB bog sensitivity (Table 3) are attributable to the model's structure where homogeneous vegetation and soil functions are included in both the upland and wetland version. Some exogenous climate inputs caused large changes in simulated C flux for the forest and peatland ecosystems. Such climatic sensitivity has been reported in boreal ecosystem modelling using Wetland-DNDC (the wetland version of Forest-DNDC: Zhang *et al*. 2002) as well as other ecosystem models (e.g. Grant *et al*. 2008, Yuan *et al*. 2008). Sensitivity analysis reveals that the functions

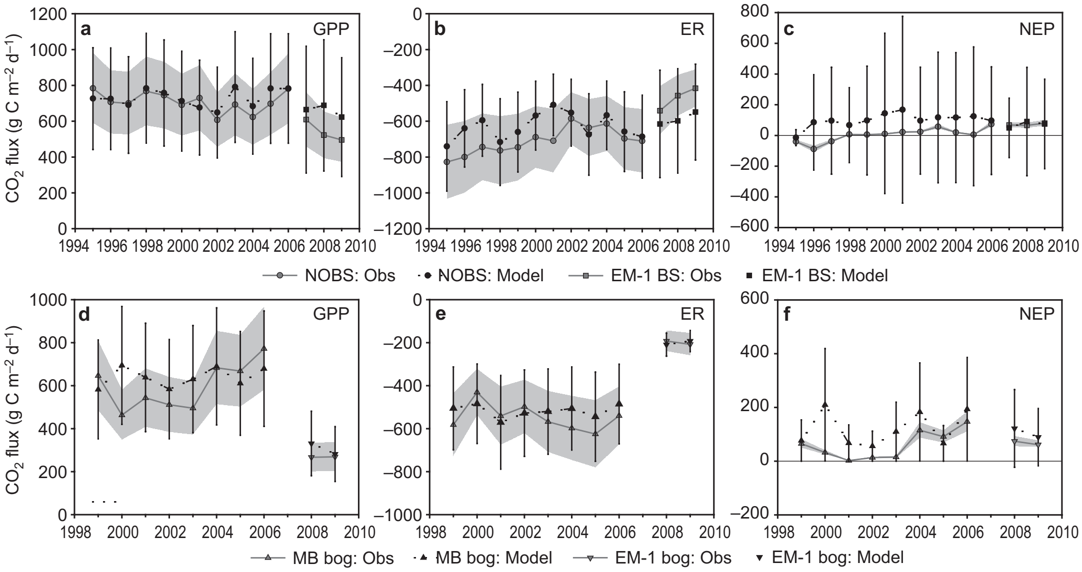

Fig. 8. Comparison between measured and modelled annual CO$_2$ fluxes (GPP, ER, and NEP) (g C m^{-2} yr^{-1}) for forest sites (**a**–**c**) and peatland sites (**d**–**f**). Obs in EM-1 bog includes partial annual flux based on the sum from DOY 170 to 365 in 2008 and from DOY 1 to 302 in 2009. Shaded areas indicate measured flux error ranges of the potential uncertainty of measurements, E_{Measured} (25% of measured flux according to Griffis *et al.* 2003). Error bars indicate the potential uncertainty of simulations, E_{Model}, estimated as described in the 'Model evaluation' section.

for ecosystem C flux are sensitive to only a small number of soil inputs including organic and mineral soil types (Table 3). This suggests that Forest-DNDC is generally applicable to other locations within the boreal biome with less consideration for spatial variations in soil

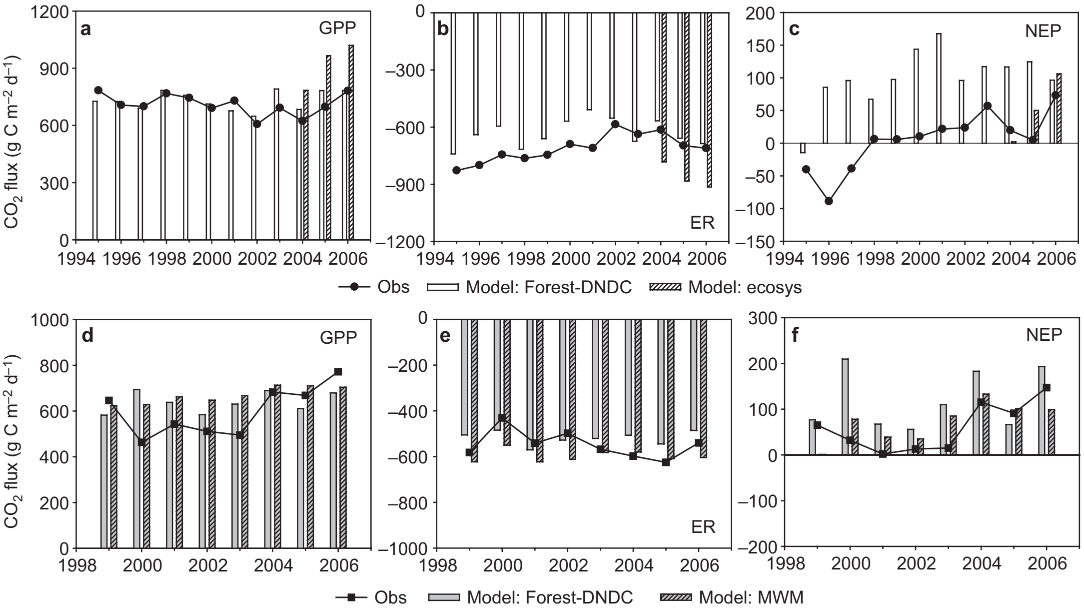

Fig. 9. Comparison of annual CO$_2$ flux (GPP, ER, and NEP) (g C m^{-2} yr^{-1}) between simulations from this study (Model: Forest-DNDC) and other modelling studies (Model: ecosys and Model: MWM), and tower measurements (Obs.) at NOBS (**a**–**c**) and MB bog (**d**–**f**).

Table 3. Sensitivity analysis of inputs in relation to annual CO_2 flux (g C m^{-2} yr^{-1}) at NOBS and MB bog. Results are provided only for five inputs that generated changes ≥ 10% or ≤ –10% in GPP or ER at either site.

Variable (unit)	Change(%)	NOBS						MB bog					
		GPP change (775[a])		ER change (736[a])		NEP change (39[a])		GPP change (552[a])		ER change (427[a])		NEP change (125[a])	
		%	g C m^{-2} yr^{-1}	%	g C m^{-2} yr^{-1}	%	g C m^{-2} yr^{-1}	%	g C m^{-2} yr^{-1}	%	g C m^{-2} yr^{-1}	%	g C m^{-2} yr^{-1}
Climate input													
Daily max temp. (°C)	20	3.0	23.5	11.9	87.4	–164.6	–63.9	–2.2	–12.2	1.5	6.3	–14.8	–18.5
	–20	–6.1	–47.6	–11.5	–84.7	95.7	37.1	–17.4	–96.2	–35.3	–150.9	43.9	54.7
Daily min temp. (°C)	20	2.7	20.7	5.2	37.9	–44.5	–17.3	–16.8	–92.5	–21.8	–93.2	0.6	0.7
	–20	–2.6	–20.4	–4.1	–30.5	25.9	10.0	–22.2	–122.3	–35.3	–150.7	22.8	28.5
Daily precip. (mm)	20	1.7	12.9	1.2	9.2	9.5	3.7	–10.3	–57.1	–30.9	–131.9	60.0	74.9
	–20	–0.2	–1.8	–0.3	–2.5	1.8	0.7	–28.0	–154.5	–42.1	–179.8	20.3	25.3
Soil													
Type of organic soil	Mull[b]	0	0.1	48.0	353.3	–910.1	–353.2	NA	NA	NA			
Type of mineral soil	Sand[c]	–14.0	–108.3	–15.6	–115.1	17.7	6.9	–0.1	–0.8	9.5	40.8	–33.3	–41.5

[a] Results of reference simulation (g C m^{-2} yr^{-1}) used in the calculation of sensitivity.

[b] Changes among three organic types prescribed in Forest-DNDC, from mor to mull for the forest site.

[c] Changes among twelve types prescribed in Forest-DNDC, from clay to sand (forest site); from silty-clay to sand (peatland site).

NA: not applicable.

and vegetation data that are the internal inputs of the model. Sensitivity tests carried out here reveal that organic and mineral soil types need to be adjusted for other locations. Therefore, our results implicate that Forest-DNDC represents C exchange from boreal forest and peatland ecosystems if precise climate data and soil information are determined.

It is assumed that discrepancies in daily CO_2 flux are related to uncertainties in the parameterization of vegetation parameters and estimated soil variables in Forest-DNDC (soil temperature and moisture). Uncertainties in parameterization are found in the evaluation of daily modelled GPP (Figs. 4–7). Simulations failed to capture the timings of increasing GPP in the earlier growing seasons and overestimated or underestimated measured GPP in the mid-growing seasons. Phenological parameters for woody and ground vegetation in Forest-DNDC (e.g. GDDFolStart, GDDWoodStart, GDDmax, GDDmin, and GDDopt: Appendix) determine the timing of photosynthesis onset, so the values of these parameters account for the discrepancy in GPP in the spring. For example, a clear discrepancy in GPP was present in the earlier growing seasons in EM-1 bog (Fig. 7), which is associated with the setting of phenological parameters for woody vegetation that led to the earlier start of woody vegetation photosynthesis in the simulations. We conducted additional sensitivity tests for GPP with vegetation parameters in Appendix (results are not shown). These tests demonstrated that all the phonological parameters provide relatively low sensitivity in annual GPP (i.e. < 10% of sensitivity). However, they can significantly affect seasonal fluctuations in C flux that are an important indicator of C cycling in response to climate change (Badeck *et al.* 2004). Another uncertainty involves parameters that are set to limit the photosynthetic rate during the mid-growing seasons (e.g. AmaxA, AmaxB, and AmaxFrac: Appendix). Since GPP predictive capacity was systematically underestimated for NOBS and MB (Figs. 4 and 6), the used parameter values produced some errors in the simulations of GPP.

Furthermore, discrepancies in C simulations could be associated with uncertainties in estimated soil temperature and moisture. Field and modelling studies in boreal ecosystems show that soil temperature and moisture explain the spatial and temporal variability in C flux (e.g. El Maayar *et al.* 2001, Bergeron *et al.* 2007). In Forest-DNDC, these soil variables affect the rates of photosynthesis and decomposition. During the growing seasons, some modelled values of GPP and ER were shown to be significantly higher or lower than the measurements (Figs. 4–7). Particularly for MB bog, years with higher measured summer GPP (2004 to 2006) are of interest because higher GPP could be suggestive of higher moisture. From precipitation records, it was revealed that the years from 2001 to 2003 had lower rainfall and very low water tables, while the years from 2004 to 2006 had higher rainfall and much shallower water tables (*see* Roulet *et al.* 2007) as compared with other years. For the same periods, lower modelled and measured GPP peaks were detected during the summer months from 2001 to 2003, while the higher peaks were detected from 2004 to 2006. Roulet *et al.* (2007) conjectured that drier conditions produced a reduction in GPP due to withering shrub leaves and desiccation of the *Sphagnum* mosses. Although Forest-DNDC does not include the persistent impact of climate on C flux (e.g. withering leaves due to drought), simulations carried out in this study seem to reflect wet soil conditions that can cause an increase in GPP.

Forest-DNDC can be useful to the study of changes in C dynamics caused by flooding because it contains details on the biogeochemical processes based on changes in redox chemistry. It supports a C flux reference in relation to undisturbed boreal ecosystems before inundation occurs. In areas flooded due to the development of reservoirs for the purposes of producing hydroelectricity, Forest-DNDC can be used to address changes in C exchange over the lifetime of the reservoir (~100 years is the anticipated life span of a hydroelectric reservoir: Gagnon and van de Vate 1997) by contrasting simulated CO_2 flux in an ecosystem without having flooding to simulations in the same ecosystem with having flooding. The C flux simulations carried out in this study (Figs. 4–7) may be a reference to the natural C exchange for 100 years if an assumption that same C flux continues in the future is applied. According to averaged simulated NEP for the study period at the study sites, natural boreal ecosystems sequester between 70 and 120 g C m^{-2} yr^{-1} during 100 years if there is no climate change and no fire occurrences. Especially for the Forest-DNDC simulation of the natural landscape C flux, burnt areas would need to be incorporated. However, we did not include the burnt areas' flux in the evaluation of NEP since we have no measurements from these surfaces. As compared with CO_2 uptakes (positive NEP) by natural boreal ecosystems, CO_2 emissions (negative NEP) of approximately 50 g C m^{-2} yr^{-1} have been reported from flooded Canadian boreal forests and peatlands (Rudd *et al*. 1993). It is suspected that this reported value contains considerable uncertainty resulting from a poor understanding of C flux transitions that occur in conjunction with the increasing age of a reservoir, i.e. higher flux rates during early stages would transition to lower flux rates as time goes on (e.g. St. Louis *et al*. 2000, Tremblay *et al*. 2004). Changes in C exchange over the EM-1 reservoir can be quantified using C flux simulations for the EM-1 ecosystems in this study (Figs. 5 and 7) and the number of an approximate CO_2 emission under flooded conditions in the boreal ecosystems (50 g C m^{-2} yr^{-1} by Rudd *et al*. 1993). If no flooding occurs under natural conditions, boreal forest and peatland ecosystems within the 603-km^2 reservoir area potentially sequester approximately 38 g C m^{-2} yr^{-1} throughout a 100-year period (66 g C m^{-2} yr^{-1} for 30% of mature forests, EM-1 BS, and 103 g C m^{-2} yr^{-1} for 18% of peatlands, EM-1 bog). The difference between the two scenarios of natural and flooded conditions is the flooding impact on the C exchange rate, evaluated as a loss of approximately 88 g C m^{-2} yr^{-1} during the life span of a reservoir (or a total of approximately 8800 g C m^{-2} for 100 years).

As a further study, C exchange under flooded conditions might be projected after adapting Forest-DNDC to flooded boreal ecosystems. However, considerable modifications of Forest-DNDC are needed to adapt it to simulate flooded ecosystems. Certain subroutines should be removed from Forest-DNDC or altered to obtain functions and parameters appropriate for the conditions of flooding, which represents the termination of terrestrial GPP and autotrophic respiration after flooding, and soil decomposition rates and soil temperatures from flooded ecosystems. Moreover, internal aquatic C processes, such as sedimentation and planktonic production and respiration, need to be added.

In conclusion, this study showed that Forest-DNDC can provide a reference for C exchange in natural boreal terrestrial ecosystems when there is a need to examine alterations in C exchange due to flooding. The simulations in this study carried out for black spruce forest and peatland ecosystems produced a reasonable range of CO_2 fluxes. Sensitivity analysis revealed that only a few climate and soil inputs in Forest-DNDC play a critical role in the variation of CO_2 flux. The model is thus easily applicable over a large area of boreal forest and peatland ecosystems. Forest-DNDC is a promising method to evaluate how much C exchange is altered after flooding based on a comparison between simulated C exchange under natural and flooded conditions.

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Appendix. Description of vegetation parameters used in this study. Default indicates default parameters for spruce type (NOBS/EM-1) and vascular plant type (MB bog/EM-1 bog) in Forest-DNDC.

Variable (unit)	Description	NOBS/EM-1 BS		MB bog/EM-1 bog	
		Value	Source	Value	Source
Woody vegetation					
AmaxA	Intercept for calculating maximum photosynthetic rate (Amax)	5.3 (9.3[a])	Wythers *et al.* 2005	5.52	Default
AmaxB	Slope for calculating Amax	21.5	Default	8.7	Default
AmaxFrac	Daily Amax as a fraction of early morning instantaneous rate	0.76 (0.73[b])	Default	0.76	Default
BaseFolRespFrac	Respiration as a fraction of maximum photosynthesis (PSN)	0.1 (0.075[a])	Wythers *et al.* 2005	0.1	Default
DVPD1	Coefficient for calculating vapour pressure deficit (VPD)	0.05	Default	0.007	Default
DVPD2	Coefficient for calculating VPD	2	Default	2	Default
FolCNR (g g^{-1})	C:N ratio in foliage and fine root	41.3 (37[a])	White *et al.* 2000	31.5	Default
FolNCon (%)	Foliage N concentration by weight	0.8 (1.2[a]; 0.6[b])	Bergeron *et al.* 2007	1.4 (1.5[c])	Moore *et al.* 2006
FolNRetrans	Fraction of foliage N retranslocated before leaf falls down	0.5	Default	0.5	Default
FolReten (yr)	Foliage retention	4	Default	2 (1.5[c])	Shaver 1981
GDDFolEnd	Growing degree days (GDD) at which foliar production ends	1200 (1100[a])	Wythers *et al.* 2005	1300	Default
GDDFolStart	GDD at which foliar production starts	300 (250[a])	Wythers *et al.* 2005	400	Default
GrespFrac	Growth respiration as a fraction of allocated C	0.25	Default	0.39	Default
HalfSat (lmol s^{-1})	Light level where PSN is 0.5Amax	250	Default	300	Default
K	Canopy light extinction constant	0.5	Default	0.58	Default
LeafGeo	Foliar geometry index	1	Default	1	Default
CFracB	Fraction of C in biomass	0.52 (0.45[a])	Y. Kim unpubl. data data	0.49 (0.45[c])	T.R. Moore unpubl. data
GDDWoodEnd	GDD at which wood production ends	1200 (1400[a])	Wythers *et al.* 2005	1300	Default
GDDWoodStart	GDD at which wood production begins	300 (250[a])	Wythers *et al.* 2005	400	Default
SLWdel (g m^{-2} g^{-1})	Change in specific leaf weight (SLW) with canopy depth	0	Default	0.2	Default

continued

Appendix. Continued.

Variable (unit)	Description	NOBS/EM-1 BS		MB bog/EM-1 bog	
		Value	Source	Value	Source
WoodCNR	C:N ratio of woody biomass	267 (200[a])	Grant *et al.* 2001	113 (100[c])	Bubier *et al.* 2007
WUEConst	Coefficient for calculating water-use efficiency	10.9 (13.9[a])	Wythers *et al.* 2005	13.9	Default
PsnTMin (°C)	Minimum temperature for PSN	0 (2[a])	Wythers *et al.* 2005	0 (–5[c])	Naumburg *et al.* 2004
PsnTOpt (°C)	Optimum temperature for PSN	20 (24[a])	Wythers *et al.* 2005	25 (23[c])	Kimball *et al.* 1997
RespQ10	Q10 value for foliar respiration	2	Default	2	Default
SLWMax (g m^{-2})	SLW at the top of canopy	200 (170[a])	Wythers *et al.* 2005	145 (285.7[c])	Moore *et al.* 2002
SenescStart	Julian day of starting senescence	270	Default	260	Default
WoodMRFrac (g C m^{-3} h^{-1})	Wood maintenance respiration as a fraction of gross PSN	0.04 (0.07[a])	Wythers *et al.* 2005	0.7	Default
WoodMaxGrow (% yr^{-1})	Maximum wood growth rate	0.9	Default	1	Default
Ground vegetation					
Amax (mg CO$_2$ g^{-1} h^{-1})	Maximum photosynthetic rate	1 (1.6[a])	Skre and Oechel 1981	1.6	Default
ExtK	Light extinction coefficient in Beer-Lambert's law	0.5	Default	0.5	Default
Fvascu	Fraction of vascular plants in groundcover (0 to 1)	0	Default	0	Default
FAI (kg C ha^{-1})	Converting plant C to area index	893	Default	893	Default
GDDmax	Maximum GDD for PSN	2300	Default	2500 (2300[c])	Zhang *et al.* 2002
GDDmin	Minimum GDD for PSN	500	Default	100 (500[c])	Zhang *et al.* 2002
GDDopt	Optimal GDD for PSN	1200	Default	1300 (1200[c])	Zhang *et al.* 2002
HalfSat (umol s^{-1})	Light level where PSN is 0.5Amax	40	Default	40	Default
RespR (mg CO$_2$ g^{-1} h^{-1})	Respiration rate at 20ºC	0.175 (0.25[a])	Skre and Oechel 1981	0.175 (0.25[c])	Skre and Oechel 1981
N0 (%)	Critical N concentration	1	Default	1	Default
SoilFrac	Fraction of biomass in soil	0	Default	0	Default
T_{max} (°C)	Maximum temperature for PSN	35	Default	35	Default
T_{min} (°C)	Minimum temperature for PSN	5 (0[a])	Kurbatova *et al.* 2009	5 (0[c])	Kurbatova *et al.* 2009
T_{opt} (°C)	Optimal temperature for PSN	20 (15[a])	Kurbatova *et al.* 2009	20 (15[c])	Kurbatova *et al.* 2009
Turnover	Annual litter production rate	0.4	Default	0.4	Zhang *et al.* 2002

[a] Default parameters for spruce type in Forest-DNDC.
[b] Derived from parameter optimization for EM-1 BS.
[c] Default parameters for vascular plant type in Forest-DNDC.