Historical and projected carbon balance of mature black spruce ecosystems across North America: the role of carbon–nitrogen interactions

J S Clein[1], A D McGuire[2], X Zhang[3], D W Kicklighter[4], J M Melillo[4], S C Wofsy[5], P G Jarvis[6] & J M Massheder[6]
[1]*Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA*
[2]*U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK, USA*
[3]*Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK, USA*
[4]*The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, USA*
[5]*Division of Applied Sciences, Harvard University, Cambridge, MA, USA*
[6]*Institute of Ecology and Resource Management, University of Edinburgh, Scotland*

Abstract

The role of carbon (C) and nitrogen (N) interactions on sequestration of atmospheric CO_2 in black spruce ecosystems across North America was evaluated with the Terrestrial Ecosystem Model (TEM) by applying parameterizations of the model in which C–N dynamics were either coupled or uncoupled. First, the performance of the parameterizations, which were developed for the dynamics of black spruce ecosystems at the Bonanza Creek Long-Term Ecological Research site in Alaska, were evaluated by simulating C dynamics at eddy correlation tower sites in the Boreal Ecosystem Atmosphere Study (BOREAS) for black spruce ecosystems in the northern study area (northern site) and the southern study area (southern site) with local climate data. We compared simulated monthly growing season (May to September) estimates of gross primary production (GPP), total ecosystem respiration (RESP), and net ecosystem production (NEP) from 1994 to 1997 to available field-based estimates at both sites. At the northern site, monthly growing season estimates of GPP and RESP for the coupled and uncoupled simulations were highly correlated with the field-based estimates (coupled: R^2 = 0.77, 0.88 for GPP and RESP; uncoupled: R^2 = 0.67, 0.92 for GPP and RESP). Although the simulated seasonal pattern of NEP generally matched the field-based data, the correlations between field-based and simulated monthly growing season NEP were lower (R^2 = 0.40, 0.00 for coupled and uncoupled simulations, respectively) in comparison to the correlations between field-based and simulated GPP and RESP. The annual NEP simulated by the coupled parameterization fell within the uncertainty of field-based estimates in two of three years. On the other hand, annual NEP simulated by the uncoupled parameterization only fell within the field-based uncertainty in one of three years. At the southern site, simulated NEP generally matched field-based NEP estimates, and the correlation between monthly growing season field-based and simulated NEP (R^2 = 0.36, 0.20 for coupled and uncoupled simulations, respectively) was similar to the correlations at the northern site. To evaluate the role of N dynamics in C balance of black spruce ecosystems across North America, we simulated historical and projected C dynamics from 1900 to 2100 with a global-based climatology at 0.5° resolution (latitude × longitude) with both the coupled and uncoupled parameterizations of TEM. From analyses at the northern site, several consistent patterns emerge. There was greater inter-annual variability in net primary production (NPP) simulated by the uncoupled parameterization as compared to the coupled parameterization, which led to substantial differences in inter-annual variability in NEP between the parameterizations. The divergence between NPP and heterotrophic respiration was greater in the uncoupled simulation, resulting in more C sequestration during the projected period. These responses were the result of fundamentally different responses of the coupled and uncoupled parameterizations to changes in CO_2 and climate.

Across North American black spruce ecosystems, the range of simulated decadal changes in C storage was substantially greater for the uncoupled parameterization than for the coupled parameterization. Analysis of the spatial variability in decadal responses of C dynamics revealed that C fluxes simulated by the coupled and uncoupled parameterizations have different sensitivities to climate and that the climate sensitivities of the fluxes change over the temporal scope of the simulations. The results of this study suggest that uncertainties can be reduced through (1) factorial studies focused on elucidating the role of C and N interactions in the response of mature black spruce ecosystems to manipulations of atmospheric CO_2 and climate, (2) establishment of a network of continuous, long-term measurements of C dynamics across the range of mature black spruce ecosystems in North America, and (3) ancillary measurements in the network to elucidate the role of C and N interactions in exchange of CO_2 with the atmosphere.

Introduction

The response of the large amount of carbon (C) stored in high latitude ecosystems to projected global change has implications for the growth rate of atmospheric carbon dioxide (CO_2, McGuire and Hobbie, 1997). These responses may be classified as functional responses associated with the changes in ecosystem processes or structural responses associated with changes in vegetation distribution (Melillo et al., 1996a). There is evidence that warming is occurring in some high latitude areas (Beltrami and Mareschal, 1991; Chapman and Walsh, 1993; Osterkamp and Romanovsky, 1999; Serreze et al., 2000), and that the warming may be impacting ecosystem function and structure (Chapin et al., 1995; Kurz and Apps, 1995; Kurz et al., 1995; Oechel et al., 1993, 1995). There are several hypotheses concerning the functional response of C storage in high latitude ecosystems to potential changes in climate associated with increases in atmospheric CO_2. One hypothesis is that climate warming will release C by increasing decomposition more than net primary production (NPP), thereby feeding back to further increases in atmospheric CO_2 (Houghton and Woodwell, 1989; Oechel et al., 1993). Another hypothesis is based on the inference that soil organic nitrogen (N) mineralization will increase with decomposition rates in response to elevated temperature (e.g., see Nadelhoffer et al., 1991), and predicts that the increased availability of N to plants will lead to increased NPP in high latitude ecosystems, which are generally limited by N availability (Shaver et al., 1992). This hypothesis predicts that high latitude ecosystems will be a net sink for atmospheric CO_2 if increases in NPP are greater than releases from decomposition because vegetation has a higher C:N ratio than soil.

The hypotheses of Houghton and Woodwell (1989) and of Shaver et al. (1992) focus on the ecosystem-level responses to warming and do not consider ecosystem-level responses associated with increases in atmospheric CO_2. Although elevated CO_2 typically enhances NPP, it also reduces leaf N concentration (McGuire et al., 1995). If lower leaf N concentration results in reduced litter quality, it has the potential to depress decomposition and net N mineralization (NMIN) rates; thereby decreasing N availability and NPP (McGuire et al., 1995, 1997). There is also evidence that production of N-limited plants is less responsive to increases in CO_2 (McGuire et al., 1995). Since warming and elevated CO_2 can each influence NPP and decomposition in different ways, it is important to consider how ecosystem C storage responds to simultaneous changes in climate and atmospheric CO_2.

It is not clear whether high latitude ecosystems are sequestering or releasing C, or if there is interannual variability in the source–sink activity of high latitudes (Chapin et al., 2000). Carbon storage in black spruce (*Picea mariana* (Mill.) ecosystems, which are prevalent throughout much of the North American boreal zone (Larson, 1980; Oechel and Lawrence, 1985; Van Cleve et al., 1983), has been the focus of several studies. Factors that control C storage and loss (NPP and R_H) in black spruce ecosystems include N availability (Van Cleve and Zasada, 1976; Van Nostrand, 1979; Weetman, 1975), soil temperature and moisture (Van Cleve et al., 1983, 1990), and soil organic matter quality (Flanagan and Van Cleve, 1983; Van Cleve et al., 1983). Van Cleve et al. (1990) found that experimentally warming the forest floor of a black spruce stand for three summers increased decomposition, foliar N concentration, and photosynthesis, suggesting that tree growth increased with greater N availability. Bonan and Van Cleve (1992) used a forest dynamics model (Bonan 1990a, b) to simulate how soil temperature, N mineralization and tree growth affect C fluxes in boreal forest stands. Over a 25-year period, the simulations indicate that soil warming increased decomposition, N mineralization, and C uptake by

trees, resulting in a net increase in C storage in the vegetation.

Black spruce ecosystem dynamics were a major focus of the boreal ecosystem atmosphere study (BOREAS, Sellers et al., 1997). In BOREAS, eddy correlation towers were used to measure CO_2 exchange in boreal forests (Goulden et al., 1997, 1998; Jarvis et al., 1997). The eddy correlation towers measure net ecosystem exchange, which is the difference between total respiration (RESP), including heterotrophic and autotrophic respiration, and gross primary production (GPP). Goulden et al. (1998) analyzed the eddy correlation measurements of an old black spruce stand near northern Manitoba, Canada from October 1994 to October 1997 and found the site to be an overall source during that period. The site was a source for the first two years and a weak sink during the last year (Goulden et al., 1998). A black spruce stand near Prince Albert, Saskatchewan, in Canada was a C sink over the 120-day growing season in 1994 (Jarvis et al., 1997) and over the full year in 1996 (Massheder, 2000).

A number of site-specific models have been applied to simulate the C dynamics for the BOREAS black spruce site of Goulden et al. (1998). Although simulations by these models generally reproduce the monthly variation in net fluxes measured at the site (Frolking et al., 1996, Frolking, 1997; Kimball et al., 1997; Amthor et al., 2000), the models differ with respect to structure, formulations employed, and parameterizations of formulations. In particular, several of the models are capable of simulating C dynamics without explicit consideration of the interaction between C and N dynamics. Given the important role of N dynamics in the C balance of black spruce ecosystems identified in process-based field studies, we asked the question: Does consideration of N dynamics influence the spatial and temporal responses of C dynamics in mature black spruce ecosystems to historical and projected climate variability in North America? To investigate this question, we used the Terrestrial Ecosystem Model (TEM, McGuire et al., 2000a) to evaluate the importance of considering the coupling between C and N dynamics in the responses of mature black spruce ecosystems. First, we developed black spruce parameterizations for versions of the model in which C and N dynamics were coupled and uncoupled. We evaluated the performance of these parameterizations at two eddy correlation tower sites in black spruce stands by comparing field-based C fluxes to simulated C fluxes. Next, we compared the C

dynamics between applications of the coupled and uncoupled parameterizations that simulated the response of mature black spruce ecosystems to historical and projected climate variability across the range of black spruce ecosystems in North America.

Methods

Overview

We parameterized version 4.1 of TEM for a mature black spruce ecosystem at Bonanza Creek, Alaska. We developed a second parameterization in which the N cycle was uncoupled from the C cycle in the model. To verify the parameterizations, we simulated C dynamics for the old black spruce site in the northern study area (northern site, Manitoba, Canada) of BOREAS from 1975 to 1997 using local climate data. We compared simulated monthly C fluxes (GPP, RESP, and NEP) from 1994 to 1997 to available field-based estimates (Goulden et al., 1998, as updated by Dunn et al., pers. comm., available online at: http://www.as.harvard.edu/data/boreasdata.html). As an independent test, we compared simulated monthly NEP to field-based estimates of NEP made at an old black spruce site in the southern study area (southern site, southern Saskatchewan, Canada) of BOREAS (Jarvis, pers. commun.). To evaluate the consequences of considering N feedbacks on simulated C dynamics of mature black spruce ecosystems in North America, we applied both parameterizations to simulate the response of C dynamics to historical and projected climate change from 1900 to 2100 across the range of black spruce in North America. We first analyzed the outputs for the spatial unit containing the northern site to evaluate mechanisms responsible for differences in the C dynamics simulated between the two parameterizations. Next, we evaluated spatial and temporal variability of black spruce C dynamics by comparing the spatial variation in C dynamics across North America for four different decades separated by 50-year intervals.

The Terrestrial Ecosystem Model (TEM)

The TEM is a process-based, global-scale ecosystem model that uses spatially referenced information on climate, elevation, soils, and vegetation to make monthly estimates of C and N fluxes and pool sizes of the terrestrial biosphere (Fig. 1). In this study we used version 4.1 of the model (McGuire et al., 1997; Tian
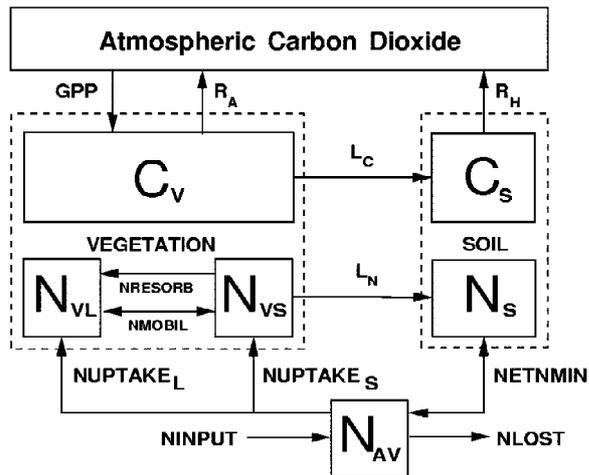
Figure 1. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation (C_V); structural N in the vegetation (N_{VS}); labile N in the vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic N in soils and detritus (N_S); and available soil inorganic N (N_{AV}). Arrows show C and N fluxes; GPP, gross primary production; R_A, autotrophic respiration; R_H, heterotrophic respiration; L_C, litterfall carbon; L_N, litterfall N; NUPTAKE$_S$, N uptake into the structural N pool of the vegetation; NUPTAKE$_L$, N uptake into the labile N pool of the vegetation; NRESORB, N resorption from dying tissue into the labile N pool of the vegetation; NMOBIL, N mobilized between the structural and labile N pools of the vegetation; NETNMIN, net N mineralization of soil organic N; NINPUT, N inputs from outside the ecosystem; and NLOST, N losses from the ecosystem.

et al., 1999) as modified by McGuire et al. (2000a), which was used to evaluate whether consideration of the effects of snowpack on winter decomposition would improve the ability of the model to simulate the seasonal cycle of atmospheric CO_2 at high latitude monitoring stations. Version 4.1 has been applied to evaluate responses of terrestrial ecosystems to historical and projected changes in atmospheric CO_2 and climate for the globe (Kicklighter et al., 1999; Melillo et al., 1996a, b; Xiao et al., 1998), the Amazon River Basin (Tian et al., 1998, 2000), the conterminous United States (Schimel et al., 2000; Tian et al., 1999), and pan-arctic tundra ecosystems (Clein et al., 2000; McGuire et al., 2000b).

For each monthly time step, NEP is calculated as the difference between NPP and heterotrophic respiration (R_H). NPP is calculated as the difference between GPP and plant autotrophic respiration. Algorithms describing calculations for R_H and plant autotrophic respiration are described elsewhere (McGuire et al., 1997, Tian et al., 1999). Monthly GPP considers the

effects of several factors and is calculated as follows:

$$GPP = C_{max} f(PAR) f(LEAF)$$
$$f(T) f(C_a, G_v) f(NA),$$

where C_{max} is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF is leaf area relative to maximum annual leaf area (phenology), T is monthly air temperature, C_a is atmospheric CO_2 concentration, G_v is relative canopy conductance, and NA is N availability. The effects of elevated atmospheric CO_2 directly affect $f(C_a, G_v)$ by altering intercellular CO_2 of the canopy (McGuire et al., 1997; Pan et al., 1998; Tian et al., 1999). Nitrogen availability also influences the ability of vegetation to incorporate elevated CO_2 into production (McGuire et al., 1997; Pan et al., 1998; Tian et al., 1999). Elevated atmospheric CO_2 decreases the N concentration of vegetation to influence the N requirements of production and decomposition (McGuire et al., 1997; Tian et al., 1999). The limiting effects of plant N status on GPP are represented by $f(NA)$. If N supply, which is the sum of N uptake and labile N in the vegetation, cannot meet the stoichiometric C to N ratio of biomass production, then GPP is reduced to meet the constraint. In the case where N supply does not limit biomass production, N uptake is reduced so that N supply meets the constraints of biomass production. In this way, the C–N status of the vegetation causes the model to allocate more effort toward either C or N uptake (McGuire et al., 1992).

Parameterization

Simulating C dynamics with TEM requires the use of monthly climatic data and soil- and vegetation-specific parameters appropriate to the soil and vegetation of the spatial unit under consideration. Although many of the parameters in the model are defined from published information (McGuire et al., 1992; Raich et al., 1991), some are determined by calibrating the model to fluxes and pool sizes of an intensively studied field site. For this application of TEM, we developed a new calibration based on studies describing the quantities of C and N in vegetation and soils, and rates of C and N fluxes for black spruce forests at the Bonanza Creek Experimental Forest, Alaska. Several adjustments to the parameterizations were made based on field-based estimates of GPP for the northern site in the BOREAS study. The specific data used to parameterize the model are described in Table 1. We made several changes to the parameters in *f(T)*

Table 1. Fluxes and pools used in the black spruce calibration of the Terrestrial Ecosystem Model (TEM)

Variable	Value	Source and comments
C_V	3250	Based on Table 2, Van Cleve et al. (1983), Oechel and Van Cleve (1986), and Gower and Ryan, (pers. commun.)
N_V	15	Based on Table 2, Van Cleve et al. (1983)
C_S	15 000	Richter et al. (2000)
N_S	505	Based on Tables 10 and 13, Van Cleve et al. (1983)
N_{AV}	0.5	Based on Weber and Van Cleve (1984)
GPP	760[1], 908[2]	See procedure described in Methods
NPP	152	Based on Table 3, Van Cleve et al. (1983)
NPPSAT	228	assume 50% saturation response
NUPTAKE	1.8	Based on Oechel and Van Cleve (1986) and the application of recycling estimates from Tables 3 and 7, Van Cleve et al. (1983)

[1] GPP used in the uncoupled parameterization.

[2] GPP used in the coupled parameterization

Units for annual gross primary production (GPP), net primary production (NPP) and annual N uptake by vegetation (NUPTAKE) are g C m^{-2} year^{-1} and g N m^{-2} year^{-1}, respectively. Units for vegetation carbon (C_V) and soil carbon (C_S) are g C m^{-2}. Units for vegetation carbon (N_V), soil N (N_S), and available inorganic N (N_{AV}) are g N m^{-2}.

of the GPP calculation by decreasing T_{min} to $-8.0°C$ to account for production at low temperatures and increasing T_{max} to 29.0°C to allow for acclimation to increases in mean monthly temperature throughout the projected period. Because we had no information on GPP for black spruce stands at Bonanza Creek, we first calibrated the rate-limiting parameter in the GPP formulation based on comparisons between simulated annual GPP and tower-based annual GPP for 1995 and 1996 at the northern site. We then calibrated the other rate-limiting parameters for C and N processes in the model so that it reproduced the fluxes and pools in Table 1.

For the parameterization in which the C cycle was uncoupled from the N cycle, the calibration procedure was conducted with a version of the model that did not allow any feedback of N availability on C uptake or of litter quality on decomposition. In the uncoupled version of the model, f(NA) in the GPP formulation is set equal to 1. For the response of the uncoupled simulations to be comparable with those of the coupled simulations, we adjusted the parameter C_{max} in the uncoupled calibration so that the baseline NPP of the calibration site was identical for both the coupled and uncoupled versions of TEM. This procedure produced different estimates of annual GPP in the coupled and uncoupled parameterizations.

Evaluation of Parameterizations

After parameterizing the model for both the coupled and uncoupled scenarios (Table 1), we compared the field-based fluxes of the northern and southern sites with the fluxes simulated by each of the parameterizations. For simulations at the northern site, we used local climate data (air temperature and precipitation) from 1975 to 1997 that were obtained from the Canadian AES station located 40 km east of the site (Thompson Airport). Simulations at the southern site were run with climate data from Nipawin, the Canadian AES station near the southern tower site. Estimates of GPP, RESP and NEP at the northern tower site were based on observations obtained at a half-hour resolution. The half-hour flux estimates were aggregated to approximately four-day means (Dunn et al., pers. comm., available online at: http://www-as.harvard.edu/data/boreasdata.html) and were then aggregated to monthly values for comparison with the C fluxes simulated by TEM. Half-hour observations of NEP from the southern tower site were aggregated to a monthly resolution by Massheder (pers. commun.). Gross primary production and RESP were not evaluated at the southern site because they were not available.

Application to black spruce ecosystems across North America

To examine spatial variability in C responses to climate change, we represented black spruce ecosystems across North America with the 1758 grid cells that represent boreal forests in North America north of 50° N at 0.5° resolution (latitude × longitude). We simulated C dynamics with the coupled and uncoupled versions

of TEM from 1900 to 2100, with the historical period spanning from 1900 to 1994 and the projected period spanning from 1995 to 2100. This application of TEM required that we organize a number of input data sets. In any particular year, CO_2 is assumed to be constant across all grid cells, but varies temporally from 1900 to 2100. Other variables organized for these grid cells include vegetation, elevation (NCAR/Navy, 1984), soil texture (FAO-UNESCO, 1971), cloudiness, air temperature and precipitation (Cramer, pers. commun.; update of Leemans and Cramer, 1991).

Historical CO_2 data were from Enting et al. (1994) who reported CO_2 concentrations increasing from 296 ppmv in 1900 to 361 ppmv in 1994. Projected CO_2 (1995 to 2100) was derived from the radiative forcing used by the Hadley Center CM2 simulation, which is based on the heat-trapping potential equivalent to a 1% annual increase in atmospheric CO_2 (Mitchell et al., 1995). We assumed that atmospheric CO_2 accounts for 70% of the radiative forcing in the projected period. Thus, from 1995 to 2100 we increased atmospheric CO_2 by 0.7% annually starting with 361 in 1994. We assumed all vegetation to be mature black spruce, which allowed us to evaluate the potential of black spruce ecosystems across North America to act as a C source or sink.

Historical temperature and precipitation anomalies from 1900 to 1994 were developed to 0.5° spatial resolution at the Max-Planck Institute for Meteorology (Heimann, unpubl. data) by interpolating the temperature anomalies of Jones (1994) and the precipitation anomalies of Hulme (1995). We added the monthly temperature and precipitation anomalies to the long-term monthly air temperature and precipitation database precipitation (Cramer, pers. commun.; update of Leemans and Cramer, 1991) to create historical temperature and precipitation data from 1900 to 1994. Data sets for projected climate (1995–2100) were based on monthly temperature and precipitation ramps defined from a transient simulation of the Hadley Center CM2 model as described in McGuire et al. (2000b). The CM2 simulation we used considered the radiative forcing associated with the combined effects of changes in greenhouse gases and sulphate aerosols (Mitchell et al., 1995).

To initialize each simulation, we ran TEM to equilibrium for each grid cell using average climate between 1900 and 1930. For each grid cell, average climate between 1900 and 1930 was calculated for each month of the year as the mean monthly temperature and precipitation for the first 30 years of the

Table 2. Proportion of variation explained by the linear regression between tower-based (dependent variable) and simulated C fluxes (independent variable) at the northern and southern sites. Comparisons are for values from May through September 1994, 1995, 1996 and 1997 for the northern site, and from May to September 1994 and 1996 for the southern site.

Site	Flux	Parameterization	R^2
Northern Site	GPP	Coupled	0.77
		Uncoupled	0.67
	RESP	Coupled	0.88
		Uncoupled	0.92
	NEP	Coupled	0.40
		Uncoupled	0.00
Southern Site	NEP	Coupled	0.36
		Uncoupled	0.20

simulation. The equilibrium December pools of C and N estimated for this climate were used as the initial conditions for simulating the temporal dynamics of C storage from 1901 to 2100 in each simulation.

Results

Simulated C dynamics with local climate

Over the period 1975 to 1997, the northern site experienced cooler and wetter weather than the southern site. The mean annual temperature was −3.3° C at the northern site and 0.6° C at the southern site. Mean summer temperature, defined as the average of June, July, and August, was 14.1 and 16.3°C over this period at the northern and southern sites, respectively. The long-term annual precipitation at the northern site (504 mm) was greater than at the southern site (435 mm).

At the northern site, growing season estimates (May–September) of simulated monthly GPP and RESP in both the coupled and uncoupled simulations were highly correlated with tower-based estimates of GPP and RESP (Table 2, Fig. 2a, b). Although the simulated seasonal pattern of NEP generally matched the field-based data (Fig. 3a), the correlations between field-based and simulated growing season NEP were lower than correlations between field-based and simulated GPP and RESP (Table 2). At the southern site, estimates of simulated monthly NEP generally matched field-based NEP estimates (Fig. 3b). In general at both sites, the ability of the coupled parameterization to simulate the monthly field-based C fluxes
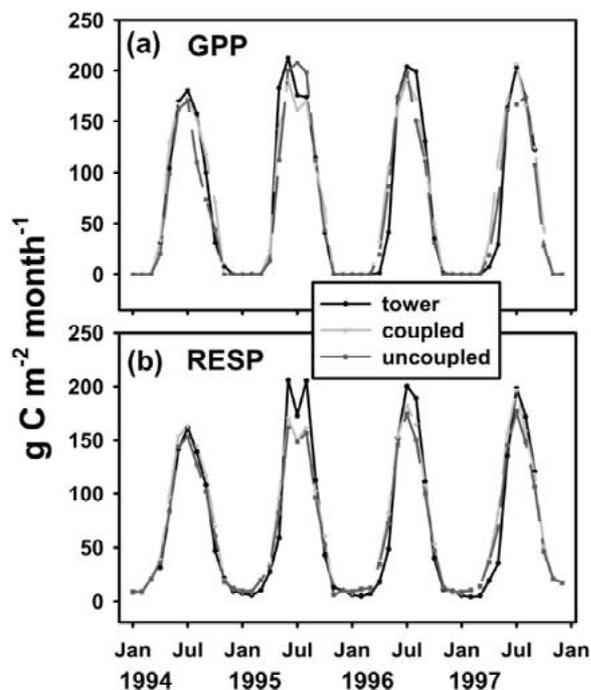
Figure 2. Field-based and simulated monthly variation in (a) gross primary production (GPP) and (b) total ecosystem respiration (RESP) for the northern site. Simulations were driven with local climate.
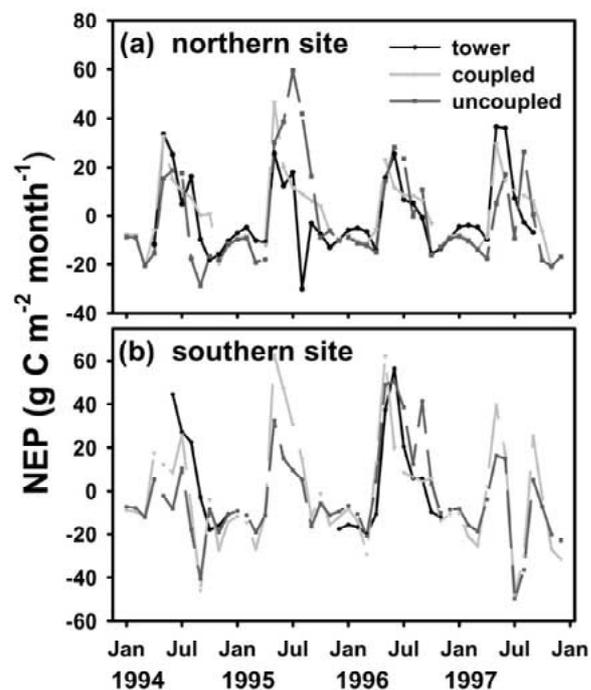

Figure 3. Field-based and simulated monthly variation in net ecosystem production (NEP) for (a) the northern site and (b) the southern site. Simulations were driven with local climate.

Table 3. Annual estimates of simulated and tower-based net ecosystem production in the northern and southern sites. Positive values indicate net C storage to the terrestrial ecosystem and negative values indicate net releases to the atmosphere.

	Northern Site			Southern Site		
	Coupled	Uncoupled	Tower	Coupled	Uncoupled	Tower
1994	−8	−95		−64	−117	
1995	32	104	−42	51	−30	
1996	−3	−10	−19	45	144	16
1997	−16	−67	21	−111	−146	

was somewhat better than the uncoupled parameterization, although both parameterizations picked up the general trends.

Simulations with both parameterizations predicted that the northern site was a source of CO_2 to the atmosphere in 1994, 1996 and 1997, and a sink for atmospheric CO_2 in 1995 (Table 3). Although applications of the two parameterizations agree on the years of source–sink activity, the simulated inter-annual variation is larger for the uncoupled parameterization. The simulated source–sink relationships agree with the field-based estimates of a source in 1996, but disagree with the field-based estimates of a source in 1995 and sink in 1997. Given uncertainties of ±50 g C m^{-2} year^{-1} in the field-based estimates at the northern site (Goulden et al., 1998), NEP simulated by the coupled parameterization falls within the uncertainty in two of the three years of available data, while NEP simulated by the uncoupled parameterization falls within the uncertainty in only one year (1996). Assuming the same uncertainty for the southern site, NEP simulated by the coupled parameterization falls within the uncertainty in 1996 (the only year with an annual estimate) while NEP simulated by the uncoupled parameterization does not (Table 3).

In the southern site, applications of the two parameterizations agree on source–sink activity in three out of four years, but the simulated inter-annual variation is larger for the uncoupled parameterization. In comparison to the simulations at the northern site, the simulations at the southern site suggest that there is substantial spatial variability in source–sink activity (Table 3).

Simulated C dynamics for historical gridded climate at the northern site

For the 0.5° grid cell that contains the northern site, the gridded data from the globally based historical
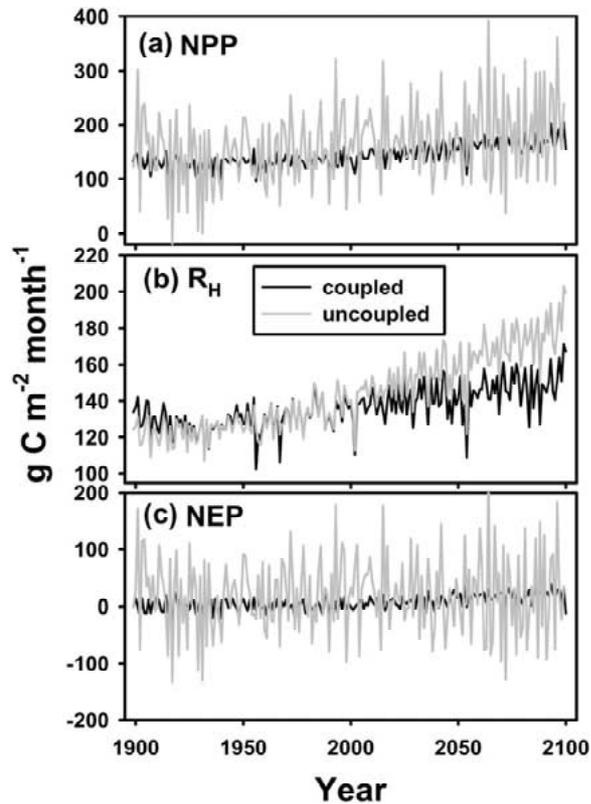
Figure 4. Historical and projected interannual variation in (a) net primary production (NPP), (b) heterotrophic respiration (R_{H}), and (c) net ecosystem production (NEP) for the northern site grid cell from the simulations by the coupled and uncoupled parameterizations of TEM.

data set indicate that the mean annual temperature for the periods from 1975 to 1997 ($-2.9°$ C) and from 1900 to 1994 ($-3.4°$ C) are similar to the local temperature. Similarly, mean summer temperature for the periods from 1975 to 1997 ($14.0°$ C) and from 1900 to 1994 ($13.8°$ C) are similar to the local temperature. Mean annual precipitation of the northern site grid cell between 1975 and 1997 (421 mm) and between 1900 and 1994 (407 mm), however, was somewhat less than the local precipitation.

Equilibrium estimates of annual NPP for the northern site grid cell were similar for both parameterizations (coupled, 133 g C m^{-2} year^{-1}; uncoupled, 123 g C m^{-2} year^{-1}). Throughout the historical period, NPP estimated by the coupled parameterization varies between 74 and 157 g C m^{-2} year^{-1} (Fig. 4a). The inter-annual variation of simulated NPP is associated with inter-annual variation in NMIN, but is not correlated with temperature or soil moisture (Table 4). In contrast to the coupled version, the inter-annual vari-

ability of NPP estimated by the uncoupled version is much greater and fluctuates between -20 and 320 g C m^{-2} year^{-1} (Fig. 4a), and is weakly correlated to soil moisture (Table 4).

Equilibrium estimates of annual R_{H} were similar for both parameterizations (coupled, 134 g C m^{-2} year^{-1}; uncoupled, 124 g C m^{-2} year^{-1}). In contrast to NPP, inter-annual variation in R_{H} estimated by the coupled version is similar to the variation estimated by the uncoupled version ($r^2 = 0.70$, Fig. 4b). For the historical period, NMIN is strongly related to R_{H} in the coupled simulation (Table 4). For both versions of TEM, R_{H} is weakly correlated to mean annual temperature and soil moisture (Table 4).

Annual NEP, (the difference between NPP and R_{H}), is approximately zero (-1 g C m^{-2} year^{-1}) at the beginning of both simulations, indicating that both versions were in equilibrium prior to simulating C dynamics. Over the historical period, the coupled version estimates that mean C storage at the northern site increased slightly by 1 g C m^{-2} year^{-1}, while the uncoupled simulation estimates an increase of 17 g C m^{-2} year^{-1} (Fig. 4c). The difference in C storage simulated by the two parameterizations is primarily associated with differences in simulated NPP. In the coupled version of TEM, changes in R_{H} kept pace with changes in NPP, so that C storage did not change much across the period. In contrast, NPP simulated by the uncoupled parameterization increased at a faster rate than R_{H}. The lower NPP response in the simulation by the coupled parameterization appears to be associated with constraints of available N on GPP.

The simulation of the coupled parameterization indicates that vegetation C decreased slightly between 1900 and 1994 (Fig. 5a). Although the uncoupled simulation indicates a slight decrease in vegetation C between approximately 1920 and 1940, it increased after 1940 and throughout the remainder of the historical period so that simulated vegetation C experienced an overall increase across the historical period (Fig. 5a). Both parameterizations estimate that soil C increased over the historical period, but the uncoupled simulation estimates increases that were approximately five times greater than estimated by the coupled simulation (Fig. 5b). The simulated cumulative change in ecosystem C, which is the sum of changes in vegetation C and soil C, is substantially lower in the coupled parameterization as compared to the uncoupled parameterization (Fig. 5c).

Table 4. Proportion of variation explained by correlation of simulated annual net primary production (NPP) and annual heterotrophic respiration (R_H) in the northern site during the historical and projected periods with other variables including mean annual temperature (MAT), and mean annual soil moisture (MASM) for the coupled and uncoupled parameterizations and annual net nitrogen mineralization (NMIN) for the coupled parameterization. The variation explained in the table was determined from independent regression analyses for each dependent variable, and does not represent the partitioning of variance among dependent variables.

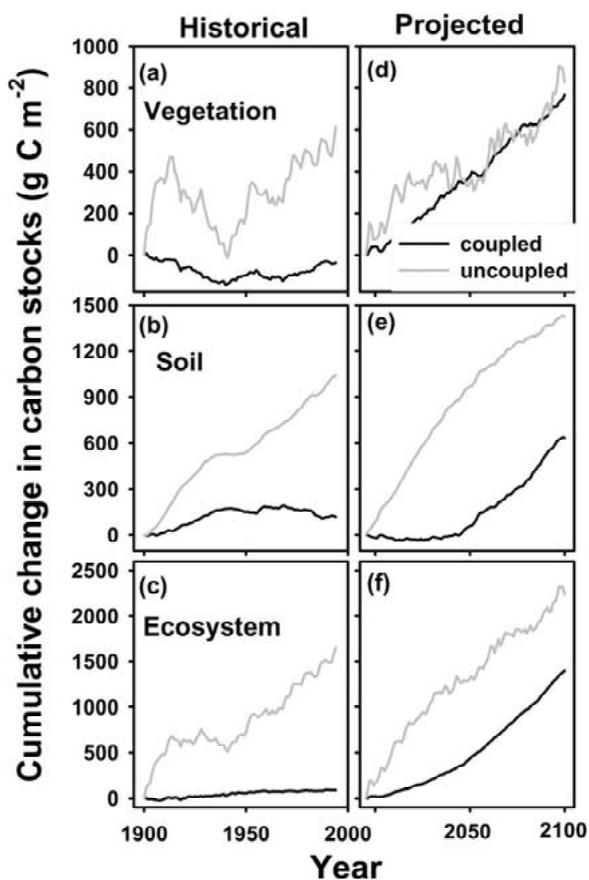| Parameterization	Flux	Historical period (n = 94 years)			Projected period (n = 106 years)		
		MAT	MASM	NMIN	MAT	MASM	NMIN
Coupled	NPP	< 0.10	<0.10	0.53	0.50	<0.10	0.61
	R_H	0.11	0.22	0.73	0.39	<0.10	0.74
Uncoupled	NPP	< 0.10	0.25	–	<0.10	<0.10	–
	R_H	0.18	0.11	–	0.64	< 0.10	–

Figure 5. Historical and projected changes in (a,d) vegetation C, (b,e) soil C, and (c,f) ecosystem C for the northern site grid cell simulated by the coupled and uncoupled parameterizations of TEM. Changes in C stocks are expressed as the change in g m^{-2} since 1900 for the historical period, and since 1995 for the projected period.

Simulated C dynamics for projected gridded climate at the northern site

Applications of both parameterizations estimate that NPP in the northern site grid cell increases slightly over the course of the projected period. Simulated mean annual NPP across the period is lower for the coupled parameterization (156 g C m^{-2} year^{-1}) in comparison to the uncoupled parameterization (180 g C m^{-2} year^{-1}). Similar to the historical period, interannual variation in NPP simulated by the uncoupled parameterization is much greater than that simulated by the coupled version (Fig. 4a). In contrast to the historical period, NPP estimated by the coupled simulation is sensitive to temperature (Table 4). For the coupled simulation, the strength of the correlation between NPP and NMIN is stronger in the projected period than in the historical period (Table 4).

Although estimates of R_H are highly correlated between the coupled and uncoupled simulations (r^2 = 0.76) and are similar at the beginning of the projected period (coupled, 138 g C m^{-2} year^{-1}; uncoupled, 141 g C m^{-2} year^{-1}), by the end of the period, R_H estimated by the coupled simulation is lower (167 g C m^{-2} year^{-1}) than R_H estimated by the uncoupled simulation (200 g C m^{-2} year^{-1}). As in the historical period, R_H in the coupled simulation is strongly related to NMIN in the projected period. Because NPP in the coupled simulation depends substantially on NMIN, the relationship between NMIN and R_H in the projected period explains similarities in the temporal pattern of NPP simulated by the coupled parameterization. Estimates of R_H by both parameterizations were sensitive to mean annual temperature (Table 4).

For the projected period, the coupled simulation estimates that annual NEP ranges from −12 to 40

g C m^{-2} year^{-1}, and that C storage increases 13 g C m^{-2} year^{-1}. The uncoupled simulation estimates that annual NEP ranges from -200 to 233 g C m^{-2} year^{-1}, an 8-fold greater range than the coupled simulation, and that C storage increases 20 g C m^{-2} year^{-1} (Fig. 4c). The difference in NEP between the two simulations (13 and 20 g C m^{-2} year^{-1}) translates to differences in cumulative C storage of 1401 g C for the coupled simulation and 2243 g C for the uncoupled simulation.

The coupled and uncoupled simulations estimate similar increases in vegetation C during the projected period (767 g vs. 825 g C m^{-2}). Thus, the difference in cumulative ecosystem C storage between the coupled and uncoupled simulations is primarily associated with differences in cumulative soil C storage estimated by the two simulations (coupled, 634 g C m^{-2} vs. uncoupled, 1418 g C m^{-2}). During the first 50 years of the projected period, the cumulative change in soil C in the coupled simulation is relatively stable near zero, after which it increases linearly for the remainder of the period (Fig. 5e). In contrast, the uncoupled simulation estimates a large increase in cumulative soil C storage over the entire projected period (Fig. 5e). The pattern of cumulative change in ecosystem C simulated by the coupled parameterization is similar to the pattern of cumulative change in vegetation C for the first 50 years of the projected period because the soil C storage was minimal, followed by 50 years with a much steeper increase in the cumulative change of ecosystem C. In contrast, the pattern of cumulative change in ecosystem C simulated by the uncoupled parameterization increases approximately in a linear fashion over the course of the projected period (Fig. 5f).

To evaluate the relative roles of increases in CO$_2$ and climate, we conducted two additional simulations that examined C storage responses of the two parameterizations to each of these variables alone during the projected period. In the CO$_2$-only simulations, we used the projected atmospheric CO$_2$ concentration with the 1900 climate throughout the projected period. In the climate-only simulation, we used the projected climate with the 1900 concentration of atmospheric CO$_2$ throughout the projected period. Over the projected period in the CO$_2$-only simulations, the uncoupled parameterization simulated over three times more ecosystem C storage than the coupled simulation, with over five times more vegetation C storage and over three times more soil C storage (Table 5). Because the responses of GPP and NPP in the coupled simulation

Table 5. Projected changes in soil C, vegetation C, and ecosystem C for the northern site grid cell from the simulations with changes in CO$_2$ only, climate only and the combination of CO$_2$ and climate for both versions of TEM. Changes in C stocks are expressed as the change in g m^{-2} since 1995 for the projected period. Positive values indicate net storage to the terrestrial ecosystem and negative values indicate net releases to the atmosphere.

Parameterization/	Projected period (n = 106 years)		
Simulation	Soil	Vegetation	Ecosystem
Coupled			
CO$_2$ only	1168	273	1441
Climate only	-573	148	-425
CO$_2$ + climate	634	767	1401
Uncoupled			
CO$_2$ only	3102	1612	4714
Climate only	-1341	-559	-1900
CO$_2$ + climate	1418	825	2243

were constrained by N dynamics, the changes in both vegetation and soil C storage were lower than in the uncoupled simulation. In the climate-only simulations, both models simulate a loss of ecosystem C during the projected period, but the losses are about four times greater in the uncoupled simulation (Table 5). Although both parameterizations predict losses of soil C, the coupled simulation estimates that vegetation C increases while the uncoupled simulation estimates that vegetation C decreases (Table 5). In the coupled simulation, the increase in vegetation C is associated with a net transfer of N from the soil to the vegetation because of increased NMIN caused by climatic warming. The gain in vegetation C does not completely compensate for the loss of soil C as the C:N ratio of the vegetation decreases from 211 to 201 across the projected period in response to the increased N availability associated with climatic warming. In this simulation the soil C:N decreased from 29.7 to 28.1 across the projected period. The different responses of C storage to CO$_2$ and climate between the coupled and uncoupled simulations at the northern site grid cell have implications for responses at the continental scale.

Temporal and spatial variation in climate across the range of black spruce in North America

During the historical period, mean annual temperature from our gridded climate data fluctuates between -4 and -1 ° C with a standard deviation of about
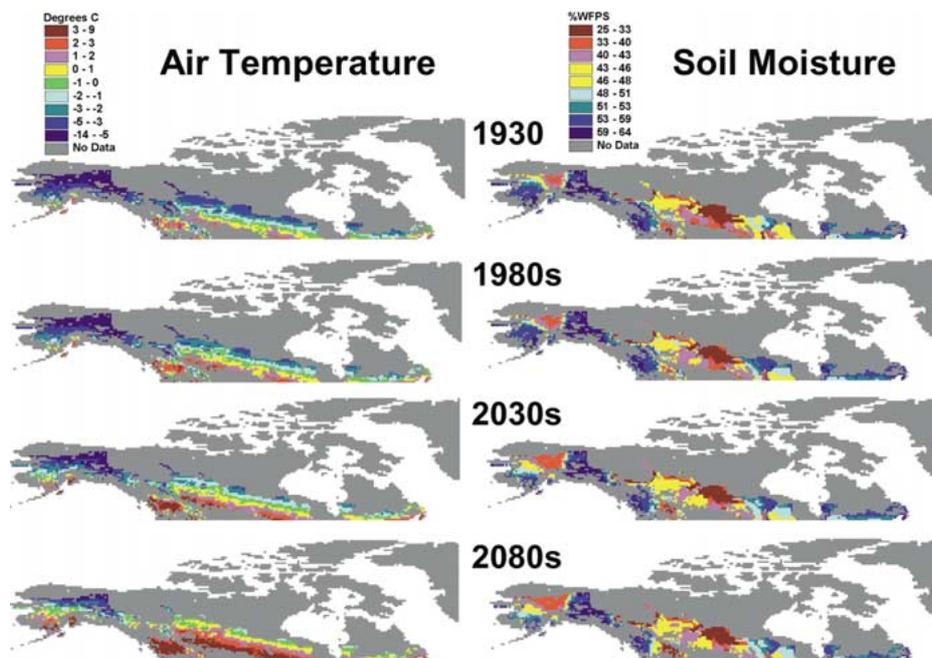
Figure 6. Spatial distribution of mean annual air temperature as °C and simulated mean annual soil moisture as percent water-filled pore space (%WFPS) across the range of North American black spruce ecosystems during four decades separated by 50 years during the simulation period 1900–2100: (a) 1930–1939, (b) 1980–1989, (c) 2030–2039, and (d) 2080–2089.
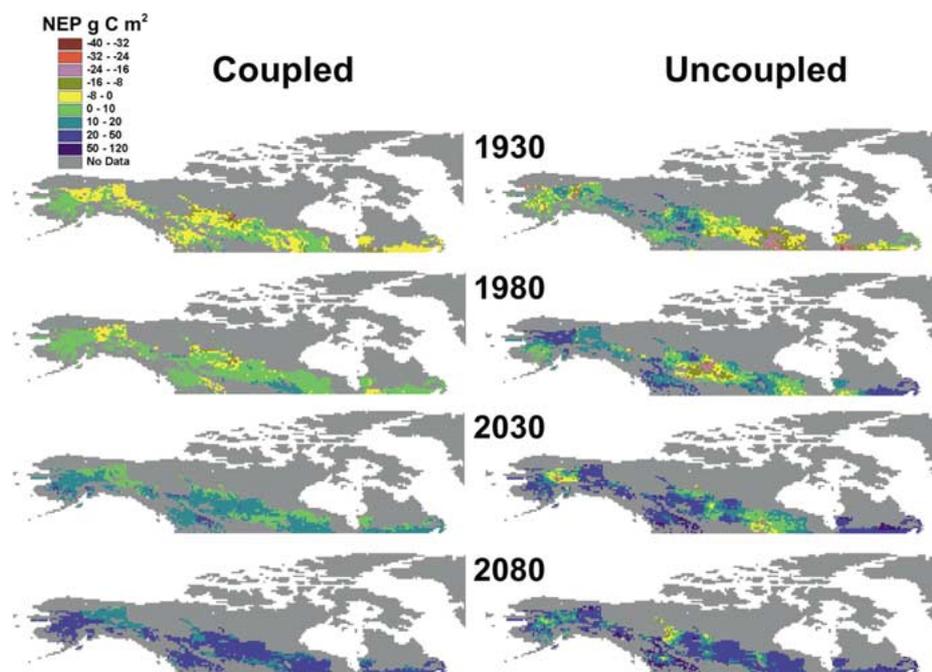

Figure 7. Simulated spatial and temporal variability in mean annual net ecosystem production (NEP) for the coupled and uncoupled parameterizations of TEM across the range of North American black spruce ecosystems during four decades separated by 50 years during the simulation period 1900–2100: (a) 1930–1939, (b) 1980–1989, (c) 2030–2039, and (d) 2080–2089.

$3°$ when spatially aggregated for the range of black spruce ecosystems in North America. Across the projected period, mean annual temperature increases from -2 to approximately $2°$ C with a standard deviation of about $3°$C above and below the mean for this spatial aggregation. For the four decades separated by 50 years during the simulation period, temperature increases north to south as expected (Fig. 6). During all decades, northern Alaska and the Yukon have lower mean annual temperatures than the rest of North America.

Across the range of black spruce ecosystems in North America, simulated soil moisture fluctuates between 45 and 50% WFPS over the course of the entire simulation. During the historical period, soil moisture was fairly stable at 48% WFPS, but during the projected period, there was a slight decrease to about 45% WFPS. Spatial variability of simulated soil moisture had a standard deviation of 10% throughout the historical and projected periods. Simulated soil moisture in North American black spruce ecosystems increases in some areas between the early and late decade in the historical period, and decreases in some areas over the two decades in the projected period (Fig. 6). In general, the spatial pattern of soil moisture in the projected decades is similar to the spatial pattern in the last decade of the historical period.

Temporal and spatial variability in simulated C dynamics across the range of black spruce in North America

The simulated response of NEP to changes in CO_2 and climate by both the coupled and uncoupled parameterizations indicate that C storage of mature black spruce ecosystems increases through the historical and projected periods (Fig. 7). However there is greater variation in the uncoupled simulation. The larger general response of C storage in the uncoupled simulation is associated with differences in the responses of NPP and R_H to increasing temperature and CO_2. In the projected period, simulated NPP and R_H increased in both simulations, but they diverged more in the uncoupled simulation.

Although the gradual increase in simulated C storage for mature black spruce ecosystems in North America through the historical and projected periods can be observed in the decadal NEP patterns of four different decades separated by 50 years (Fig. 7), changes do not occur uniformly across all regions. Also, there is substantial variation in each

decade between estimates of C storage simulated by the coupled and uncoupled parameterizations. For example, for the 1930s, the uncoupled simulation shows substantial releases of C in the region of western Ontario and eastern Manitoba, while the coupled version exhibits both a slight release and slight storage of C. For the 2030s, the coupled simulation predicts C storage across the black spruce ecosystems. In contrast, the uncoupled simulation predicts several small regions releasing C to the atmosphere.

To examine the spatial sensitivity of coupled and uncoupled simulations to climate and CO_2 across the range of black spruce ecosystems in North America, we compared the proportions of variation in decadal patterns of NPP, and R_H explained by decadal patterns of temperature and soil moisture (Table 6). For the coupled simulation, NPP and R_H were correlated with temperature in each of the decades analyzed. For the coupled simulation, the correlations of NPP and R_H with soil moisture were weak. In contrast, for the uncoupled simulation R_H was strongly correlated with soil moisture. Spatial variability in mean annual NEP simulated by both versions of TEM is not correlated with either mean annual temperature or mean annual soil moisture in any of the decades analyzed. Although the proportion of spatial variation explained by the correlations of decadal C fluxes with temperature and soil moisture do not substantially differ among the decades that we analyzed for each of the simulations, the slopes and intercepts for regressions of decadal carbon fluxes with temperature and soil moisture are different for each decade (data not shown). Thus, our results indicate that the C fluxes simulated by the coupled and uncoupled parameterizations have different sensitivities to climate and that the climate sensitivities of the fluxes change over the temporal scope of the simulations.

Discussion

Below, we first discuss insights on the temporal dynamics of C storage gained from applications of our TEM parameterizations at the northern and southern BOREAS sites. We then discuss implications of interactions between C and N dynamics at large spatial scales identified from applications of the parameterizations across black spruce ecosystems in North America.

Responses of C dynamics at the northern and southern sites

Although the correlation of growing season monthly variation in C fluxes between field-based and model-based estimates did not differ substantially between the two parameterizations, we identified differences in ranges of inter-annual variability and the long-term responses of C storage between the coupled and uncoupled simulations. The larger range of inter-annual variability simulated for the northern site by the uncoupled parameterization was mainly due to greater sensitivity of NPP to inter-annual variability in climate. Greater sensitivity of NPP to climate has also been observed in simulations of some models that do not consider C–N coupling in model comparisons of black spruce dynamics at the northern site (Amthor et al., 2001; Potter et al., 2001) and in model comparisons at the global scale (McGuire et al., 2001). Analyses of atmospheric data (Braswell et al., 1997) and stand-level and global-scale modeling analyses (Schimel et al., 1996; Vukicevic et al., 2001) also suggest that N dynamics may play a role in the response of C exchange with the atmosphere to inter-annual variability in temperature. Unfortunately, there is insufficient stand-level data on both C and N dynamics to evaluate how inter-annual variability in C dynamics may be influenced by C and N interactions. Thus, our simulations and other analyses indicate that research effort should be focused on elucidating how C and N interactions influence inter-annual variability in C dynamics of high latitude ecosystems.

In our simulations, differences in the long-term responses of C storage for the northern site grid cell between the coupled and uncoupled parameterizations were related to the different sensitivities of the parameterizations to CO_2 and climate. In both the coupled and uncoupled CO_2-only simulations, the increases in vegetation C and soil C were consistent with the results of the modeling study of Peng and Apps (1998). The CO_2-only simulations revealed that changes in C storage estimated by the coupled parameterization were less than estimated by the uncoupled parameterization because the response of GPP was constrained by N dynamics. In comparison to the uncoupled simulation, the constrained GPP response in the coupled simulation caused a lower increase in vegetation C, which led to a lower increase in soil C. Similar to the modeling studies of McGuire et al. (1997) and Peng and Apps (1998), part of the soil C response in the coupled simulation was related to increased C:N

Table 6. Proportion of variation explained by correlation of simulated mean annual net primary production (NPP) and heterotrophic respiration (R_H) of North American black spruce ecosystems for the coupled and uncoupled simulations during different decades of the historical and projected periods with other variables including mean annual temperature (MAT) and mean annual soil moisture (MASM). The proportion of variation explained by correlation of net ecosystem production for both simulations and in all decades with both variables was <0.02 for all comparisons. The variation explained in the table was determined from independent regression analyses for each dependent variable, and does not represent the partitioning of variance among dependent variables.

		Coupled simulation		Uncoupled simulation	
		MAT	MASM	MAT	MASM
1930 – 1939	NPP	0.16	< 0.10	< 0.02	< 0.10
	R_H	0.36	0.13	< 0.10	0.48
1980 – 1989	NPP	0.35	0.10	< 0.02	0.10
	R_H	0.47	0.13	< 0.02	0.45
2030 – 2039	NPP	0.27	< 0.10	< 0.02	< 0.10
	R_H	0.45	< 0.10	< 0.02	0.47
2080 – 2089	NPP	0.31	< 0.10	< 0.02	< 0.10
	R_H	0.42	< 0.10	< 0.02	0.46

of litter that retarded decomposition. The response of vegetation C is consistent with the substantial experimental evidence indicating that production of N-limited plants is less responsive to increases in CO_2 (McGuire et al., 1995). Early results of the Duke FACE experiment show an increase in photosynthesis and growth increment in loblolly pine due to a 50% increase in CO_2 (DeLucia et al., 1999). Experimental studies on the response of black spruce to elevated CO_2 have primarily been conducted with seedlings (e.g., Johnson, 1993). Clearly, studies that manipulate atmospheric CO_2 and simultaneously evaluate both C and N dynamics for mature black spruce forests are needed to help elucidate the role of C–N coupling in the response of black spruce ecosystems to rising atmospheric CO_2.

In the climate-only simulations for the northern site grid cell, the response of the uncoupled parameterization was consistent with the hypothesis of Houghton and Woodwell (1989). In the coupled simulation, vegetation C increased in association with higher rates of NMIN and the transfer of N to the vegetation as predicted by the hypothesis of Shaver et al. (1992). The increase of vegetation C by the model did not compensate for losses of soil C as the C:N ratio of vegetation decreased across the course of the projected

period. The response of the coupled simulation is consistent with the results of Måakipåå et al. (1999), who reported that warming of a Scots pine forest resulted in higher vegetation C, lower soil C, and an overall decline of C storage because increases in decomposition were greater than increases in production. The higher NMIN, increase of vegetation C, and decrease of soil C in our coupled simulation are also consistent with results of the warming experiment by Van Cleve et al. (1990) and the climate-only simulations by Peng and Apps (1998). Given our current understanding of the response of C and N dynamics in high latitude soils to climatic warming, we do not know whether the long-term response of these soils to warming will be to gain or lose C to the atmosphere (Clein et al., 2000; Oechel et al., 2000). Thus, warming experiments in black spruce ecosystems need to be designed so that they provide insight on how the climatic response of soil C and N transformations influence the long-term dynamics of soil C in these ecosystems. Improving our understanding of the climatic response of C storage in black spruce ecosystems is essential to understanding how CO_2 and climate will interact to influence C storage in these ecosystems.

Both the coupled and uncoupled simulations for the northern site grid cell that considered the combined effects of rising CO_2 and climate change suggest that CO_2 fertilization significantly offsets the potential loss of soil C in response to warming enough to predict an overall increase in both vegetation C and soil C. Similar to Peng and Apps (1998), we observed that the effects of CO_2 and climate were not additive in either simulation. In the coupled simulation that considered both factors, the response of ecosystem C storage was more than additive of the single-factor simulations because of the synergistic response of vegetation C, which occurred because increases in NMIN allowed the vegetation to incorporate rising CO_2 into production. In contrast, the response of ecosystem C storage in the uncoupled simulation was less than additive of the single-factor simulations because the response of NPP to increases in CO_2 decreased at higher temperatures. Clearly, experimental studies are needed that evaluate how C and N interactions influence the response of C storage in black spruce ecosystems to the simultaneous manipulation of increasing atmospheric CO_2 and climatic warming.

Implications of C–N interactions for responses at large spatial scales

Currently, some high latitude regions are warming, some are cooling, and there is substantial interannual variability in climate (Everett and Fitzharris, 1998; Serreze et al., 2000). Climatic change at high latitudes is expected to exhibit substantial temporal and spatial variability (McGuire et al., 2000b). Previous studies with TEM indicate that site-specific studies of C storage may not be representative of ecosystem responses at large spatial scales. For example, simulated C storage by TEM in the Amazon Basin (Tian et al., 1998, 2000), which agreed with measurements of C storage made by three studies in the Amazon Basin (Fan et al., 1990; Grace et al., 1995; Miranda et al., 1997), indicates that measured changes in site-specific C storage may not be typical of a broader region because of spatial variability in climate across the region. The study by McGuire et al. (2000b) also suggests that the scaling of C dynamics to a region of arctic tundra defined by the Kuparuk River Basin in Alaska may not be representative of the C dynamics of tundra across the Pan-arctic. In this study, the coupled parameterization simulated source–sink estimates for the northern site for 1996 and 1997 that are within the uncertainty reported by Goulden et al. (1998), while the uncoupled simulation did so for 1996. Similar to other studies with TEM, both the coupled and uncoupled simulations suggest that there is substantial spatial variability in C exchange with the atmosphere during the historical and projected periods in black spruce ecosystems across North America.

Although both the coupled and uncoupled simulations predict substantial spatial variability in C storage across North America, the range of responses is much greater in the uncoupled simulation. The coupled simulation indicates that the trend in temperature is an important control over long-term responses of NPP and R_H. In contrast, the long-term responses of NPP and R_H in the uncoupled simulation are not sensitive to trends in temperature, although R_H is sensitive to trends in soil moisture. Thus, the C fluxes simulated by the coupled and uncoupled parameterizations have fundamentally different sensitivities to climate. In addition, the climate sensitivities of the fluxes changed over the temporal scope of the simulations. To reduce uncertainties, our simulations suggest that measurements of C exchange in black spruce ecosystems should occur at a number of sites across the range of black spruce ecosystems in North America, and that

these measurements need to be continuous and long-term to identify important controls over inter-annual and long-term responses of C storage. To be most useful, these sites should be located to exploit gradients in temperature and soil moisture. In addition, a number of ancillary measurements need to accompany the measurement of the net flux at each site so that the components of net C exchange can be identified and the role of N dynamics in net C exchange can be elucidated.

Conclusion

Our study focused on black spruce ecosystems because it is the dominant ecosystem type in the boreal forest of North America, and its dynamics are likely to influence the response of C dynamics in the boreal region to changes in atmospheric CO_2 and climate. We did not intend to estimate the historical and projected response of the boreal forest in North America. Because disturbance is an important component of the C dynamics of the boreal forest region, the role of fire, insect disturbance, and logging need to be considered in simulating the historical and projected responses of the boreal forest in North America (Kurz and Apps, 1999). The long-term response of C dynamics in this region may also depend on how vegetation distribution responds to climate change (McGuire and Hobbie, 1997; Smith and Shugart, 1993).

A key result of our study is that the ability of the model parameterizations to reproduce short-term measurements of C dynamics is no guarantee that they will have the same long-term responses. Although this is not a new message, and has been elucidated earlier in others studies (Clein et al. 2000; Kicklighter et al. 1999; Pan et al. 1998; Rastetter 1996; VEMAP Members, 1995), it is not generally appreciated. Another key result is that simulated C storage is spatially variable because of spatial variation in climate, and that the spatial sensitivity of C dynamics to climate can be expected to differ across decades. This is important because climatic variation at high latitudes is expected to be spatially and temporally variable. In summary our study suggests that uncertainties can be reduced through (1) factorial studies focused on elucidating the role of C and N interactions in the response of mature black spruce ecosystems to manipulations of atmospheric CO_2 and climate, (2) establishment of a network of continuous, long-term measurements of C dynamics across the range of black spruce ecosystems in North America, and (3) ancillary measurements in the network to elucidate the role of C and N interactions in CO_2 exchange with the atmosphere.

Acknowledgements

References

Amthor J S, Chen J M, Clein J S, Frokling S E, Goulden M L, Grant R F, Kimball J S, King A W, McGuire A D, Nikolov N T, Potter C S, Wang S, Wofsy S C 2001 Boreal forest CO_2 exchange and evapotranspiration predicted by nine ecosystem process models: Inter-model comparisons and relations to field measurements. J. Geophys. Res. 106, 33623–33648.

Beltrami H and Mareschal J C 1991 Recent warming in eastern Canada inferred from geothermal measurements. Geophys. Res. Lett. 18, 605–608.

Bonan G B 1990a Carbon and nitrogen cycling in North American boreal forests. I. Litter quality and soil thermal effects in interior Alaska. Biogeochemistry 10, 1–28.

Bonan G B 1990b Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. Can. J. For. Res. 20, 1077–1088.

Bonan G B and Van Cleve K 1992 Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forests. Can. J. For. Res. 22, 629–639.

Braswell B H, Schimel D S, Linder E and Moore B III 1997 The response of global terrestrial ecosystems to interannual temperature variability. Science 278, 870–872.

Chapin F S III, Shaver G R, Giblin A E, Nadelhoffer K J and Laundre J A 1995 Responses of arctic tundra to experimental and observed changes in climate. Ecology 76, 69–711.

Chapin FS III, McGuire A D, Randerson J, Pielke Sr. R, Baldocchi D, Hobbie S E, Roulet N, Eugster W, Kasischke E, Rastetter E B, Zimov S A, Oechel W A and Running S W 2000 Feedbacks from arctic and boreal ecosystems to climate. Global Change Biol. 6 (Suppl. 1), 211–223.

Chapman W L and Walsh J E 1993 Recent variations of sea ice and air temperatures in high latitudes. Bull. Am. Meteor. Soc. 74, 33–47.

Clein J S, Kwiatkowski B L, McGuire A D, Hobbie J E, Rastetter E B, Melillo J M and Kicklighter D W 2000 Modeling carbon responses of tundra ecosystems to historical and projected climate: A comparison of a fine- and coarse-scale ecosystem model

for identification of process-based uncertainties. Global Change Biol. 6 (Suppl. 1), 127–140.

DeLucia E H, Hamilton J G, Naidu S L, Thomas R B, Andrews J A, Finzi A, Lavine M, Matamala R, Mohan J, Hendrey G and Schlesinger W H 1999 Net primary production of a forest ecosystem with experimental CO_2 enrichment. Science 284, 1177–1179.

Enting I, Wigley T and Heimann M 1994 Future emissions and concentrations of carbon dioxide: key ocean/atmosphere/land analyses. CSIRO Division of Atmospheric Research Technical Paper, 31, 120 pp.

Everett J T and Fitzharris BB 1998 The Arctic and the Antarctic. *In* The Regional Impacts of Climate Change: An Assessment of Vulnerability Eds. R T Watson, M C Zinyowera, R H Moss and D J Dokken. pp 85–103. Cambridge University Press, New York.

Fan S M, Wofsy S C, Bakwin P S and Jacob D J 1990 Atmosphere–biosphere exchange of CO_2 and O_3 in the central Amazon forest. J. Geophys. Res. 95, 16851–16864.

FAO-UNESCO 1971 Soil map of the world, 1:5,000,000. FAO/UNESCO, Paris.

Flanagan P W and Van Cleve K 1983 Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Can. J. For. Res. 13, 795–817.

Frolking S 1997 Sensitivity of spruce/moss boreal forest net ecosystem productivity to seasonal anomalies in weather. J. Geophys. Res. 102, 29053–29064.

Frolking S, Goulden M L, Wofsy S C, Fan S-M, Sutton D J, Munger J W, Bazzaz A M, Daube B C, Crill P M, Aber A D, Band L E, Wang X, Savage K, Moore T and Harris R C 1996 Temporal variability in the carbon balance of a spruce/moss boreal forest. Global Change Biol. 2, 343–366.

Goulden M L, Daube B C, Fan S-M, Sutton D J, Bazzaz A, Munger J W and Wofsy S C 1997 Physiological responses of black spruce forest to weather. J. Geophys. Res. 102, 28987–28996.

Goulden M L, Wofsy S C, Harden J W, Trumbore S E, Crill P M, Gower S T, Fries T, Daube B C, Fan S-M, Sutton D J, Bazzaz A and Munger J W 1998 Sensitivity of boreal forest carbon balance to soil thaw. Science 279, 214–217.

Grace J, Lloyd J, McIntyre J, Miranda A C, Meri P, Miranda H S, Nobre C, Monteith J, Massheder J, Wright I and Gash J 1995 Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992–1993. Science 270, 778–780.

Houghton R A and Woodwell G M 1983 Global climate change. Sci. Am. 260(4), 36–44.

Hulme M 1995 A historical monthly precipitation data for global land areas from 1900 to 1994, gridded at 3.75 × 2.5 resolution. Climate Research Unit, University of East Anglia, Norwich, UK.

Jarvis P G, Massheder J M, Hale S E, Moncrieff J B, Rayment M and Scott S L 1997 Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. J. Geophys. Res. 102D, 28953–28966.

Johnson K H 1993 Growth and ecophysiological responses of black spruce seedlings under varied water and nutrient additions. Can. J. For. Res. 23, 1033–1042.

Jones P D 1994 Hemispheric surface air temperature variations: a reanalysis and update to 1993. J. Clim. 7, 1794–1802.

Kicklighter D W, Bruno M, Doenges S, Esser G, Heimann M et al. 1999 A first order analysis of the potential role of CO_2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. Tellus 51B, 343–366.

Kimball J S, Thornton PE, White M A and Running S W 1997 Simulating forest productivity and surface–atmosphere carbon exchange in the BOREAS study region. Tree Physiol. 17, 589–599.

Kurz W A and Apps M J 1995 Retrospective assessment of carbon flows in Canadian boreal forests. *In* Forest Ecosystems, Forest Management and the Global Carbon Cycle. Eds. M J Apps and D T Price, Springer-Verlag, NATO Advanced Science Institute Series.

Kurz W A and Apps M J 1999 A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Appl. 9, 526–547.

Kurz WA, Apps M J, Stocks B J and Volney W J A 1995 Global climate change: disturbance regions and tropospheric feedbacks of temperate and boreal forests. *In* Biotic Feedbacks in the Global Climate System. Eds. G M Woodwell and F T Makenzie. Oxford University Press, New York.

Larson J A 1980 The Boreal Ecosystem. Academic Press, San Diego, CA. 500 p.

Leemans R and Cramer W P 1991 The IIASA database for mean monthly values of temperature, precipitation, and cloudiness on an terrestrial grid. IIASA RR-91-18, Laxenburg, Austria.

Makipaa R, Karjalainen T, Pussinen A and Kellomaki S 1999 Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone. Can. J. For. Res. 29, 1490–1501.

Massheder J M 2000 Surface flux measurements by eddy covariance over a black spruce stand. PhD thesis, University of Edinburgh, Scotland.

McGuire A D and Hobbie J E 1997 Global climate change and the equilibrium responses of carbon storage in arctic and subarctic regions. *In* Modeling the Arctic System: A Workshop Report on the State of Modeling in the Arctic System Science Program. pp 53–54. The Arctic Research Consortium of the United States, Fairbanks, Alaska.

McGuire A D, Melillo J M, Joyce L A, Kicklighter D W, Grace A L, Moore B III and Vorosmarty C J 1992 Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochem. Cycles 6, 101–124.

McGuire A D, Melillo J M and Joyce L A 1995 The role of N in the response of forest net primary production to elevated atmospheric carbon dioxide. Annu. Rev. Ecol. Syst. 26, 473–503.

McGuire A D, Melillo J M, Kicklighter D W, Pan Y, Xiao X, Helfrich J, Moore B III, Vorosmarty C J and Schloss A L 1997 Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration. Global Biogeochem. Cycles 11, 173–189.

McGuire A D, Melillo J M, Randerson J T, Parton W J, Heimann M, Meier R A, Clein J S, Kicklighter D W and Sauf W 2000a Modeling the effects of snowpack on heterotrophic respiration across northern temperate and high latitude regions: Comparison with measurements of atmospheric carbon dioxide in high latitudes. Biogeochemistry 48, 91–114.

McGuire A D, CleinJ S, Melillo J M, Kicklighter D W, Meier R A, Vorosmarty C J andSerreze M C 2000b Modeling carbon responses of tundra ecosystems to historical and projected climate: Sensitivity of Pan-arctic carbon storage to temporal and spatial variation in climate. Global Change Biol. 6 (Suppl. 1), 141–159.

McGuire A D, Sitch S, Clein J S, Dargaville R, Esser G, Foley J, Heimann M, Joos F, Kaplan J, Kicklighter D W, Meier R A, Melillo J M, Moore B III, Prentice I C, Ramankutty N, Reichenau T, Schloss A, Tian H, Williams L J and Wittenberg U 2001 Carbon balance of the terrestrial biosphere in the twentieth century: Analysis of CO_2, climate and land-use effects with four process-based ecosystem models. Global Biogeochem. Cycles 15, 183–206.

Melillo J M, Prentice I C, Farquhar G D, Schulze E D and Sala O E 1996a Terrestrial biotic responses to environmental change and feedbacks to climate. *In* Climate Change 1995. The Science of Climate Change. Eds. J T Houghton, L G Meira Filho, B A Callander, N Harris, A Kattenberg and K Maskell. pp 445–481. Cambridge University Press, Cambridge.

Melillo J M, Houghton R A, Kicklighter D W and McGuire A D 1996b Tropical deforestation and the global carbon budget. Annu. Rev. Energy Environ. 21, 293–310.

Miranda A C, Miranda H S, Lloyd J, Grace J, Francey R J, McIntyre J A, Meir P, Riggan P, Lockwood R and Brass J 1997 Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. Plant Cell Environ. 20, 315–328.

Mitchell J F B, Johns T C , Gregory J M and Tett S F B 1995 Climate response to increasing levels of greenhouse gases and sulphate aerosols. Nature 376, 501–504.

Nadelhoffer K J, Giblin A E, Shaver G R and Laundre J L 1991 Effects of temperature and organic matter quality on C, N and P mineralization in soils from arctic ecosystems. Ecology 72, 242–253.

NCAR/Navy 1984 Global 10-minute elevation data. Digital tape available through Nat. Oceanic and Atmos. Admin., Nat. Geophys. Data Cent., Boulder, CO.

Oechel W C and Lawrence W T 1985 Taiga. *In* Physiological Ecology of North American Plant Communities. Eds. B F Chabot and H A Mooney. pp 66–94. Chapman and Hall, New York.

Oechel W C and Van Cleve K 1986 The role of bryophytes in nutrient cycling in the taiga. *In* Forest Ecosystems in the Alaskan Taiga. Eds. K Van Cleve et al. pp 121–137. Springer, New York.

Oechel W C, Hastings S J, Vourlitis G L, Jenkins M, Reichers G and Grulke N 1993 Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361, 520–523.

Oechel W C, Vourlitis G L, Hastings S J and Bochkarev S A 1995 Change in arctic CO_2 flux over two decades: Effects of climate change at Barrow, Alaska. Ecol. Appl. 5, 846–855.

Oechel W C, Vourlitis G L, Hastings S J, Zuleta R C, Hinzman L and Kane D 2000 Acclimation of ecosystem CO2 exchange in Alaskan Arctic in response to decadal climate warming. Nature 406, 978–981.

Osterkamp T E and Romanovsky V E 1999 Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost Periglac. Process. 10, 17–37.

Pan Y, Melillo J M, McGuire A D, Kicklighter D W, Pitelka L F, Hibbard K, Pierce L L, Running S W, Ojima D S, Parton W J, Schimel D S and other VEMAP members 1998 Modeled responses of terrestrial ecosystems to elevated atmospheric CO_2: A comparison of simulation be the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). Oecologia 114, 389–404.

Peng C and Apps M J 1998 Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada 2. Sensitivity to climate change. Global Biogeochem. Cycles 12, 393–402.

Potter C S, Wang S, Nikolov N T, McGuire A D, Liu J, King A W, Kimball J S, Grant R F, Frolking S E, Clein J S, Chen J M and Amthor J S 2000 Comparison of boreal ecosystem model sensitivity to variability in climate and forest site parameters. J. Geophys. Res. In review.

Raich J W, Rastetter E B, Melillo J M, Kicklighter D W, Steudler P A, Peterson B J, Grace A L, Moore B III and Vorosmarty C J 1991 Potential net primary production in South America: application of a global model. Ecol. Appl. 1, 399–429.

Rastetter E B 1996 Validating models of ecosystem response to global change. Bioscience 46, 190–198.

Richter D D, O'Neill K P and Kasischke E S 2000 Stimulation of soil respiration in burned black spruce (*Picea mariana* L.) forest ecosystems; A hypothesis. *In* Fire, Climate Change, and Carbon Cycling in the North American Boreal Forest, Eds. E S Kasischke and B J Stocks. pp 164–178. New York: Ecological Studies Series, Springer, New York.

Schimel D S, Braswell B H, McKeown R, Ojima D S, Parton W J and Pulliam W 1996 Climate and nitrogen controls on the geography and time scales of terrestrial biogeochemical cycling. Global Biogeochem. Cycles 10, 677–692.

Schimel D, Melillo J, Tian H, McGuire A D, Kicklighter D, Kittel T, Rosenbloom N, Running S, Thornton P, Ojima D, Parton W, Kelly R, Sykes M, Neilson R, Rizzo B and Pitelka L 2000 Carbon storage by the natural and agricultural ecosystems of the US (1980–1993). Science 287, 2004–2006.

Sellers P J, Hall F G, Kelly R D, Black A, Baldocchi D, Berry J, Ryan M, Jon Ranson K, Crill P M, Lettenmaier D P, Margolis H, Cihlar J, Newcomer J, Fitzjarrald D, Jarvis P G, Gower S T, Halliwell D, Williams D, Goodison B, Wickland D E and Guertin F E 1997 BOREAS in 1997: Experiment overview, scientific results, and future directions. J. Geophys. Res. 102 D24, 28731–28769.

Serreze M C, Walsh J E, Chapin F S III, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel W C, Morison J, Zhang T and Barry R G 2000 Observational evidence of recent change in the northern high-latitude environment. Climatic Change 46, 159–207.

Shaver G R, Billings W D, Chapin F S III , Giblin A E, Nadelhoffer K J, Oechel W C and Rastetter E B 1992 Global change and the carbon balance of arctic ecosystems. Bioscience 42, 433–441.

Smith T M and Shugart H H 1993 The transient response of terrestrial carbon storage to a perturbed climate. Nature 361, 523–526.

Tian H, Melillo J M, Kicklighter D W, McGuire A D, Helfrich J, Moore B III and Vörösmarty C J 1998 Effect of interannual climate variability on carbon storage in Amazonian ecosystems. Nature 396, 664–667.

Tian H, Melillo J M, Kicklighter D W and McGuire A D 1999 The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO_2 in the United States. Tellus 51B, 414–452.

Tian H, Melillo J M, Kicklighter D W, McGuire A D, Moore B III and Vörösmarty C J 2000 Climatic and biotic controls on interannual variations of carbon storage in undisturbed ecosystems of the Amazon Basin. Global Ecol. Biogeogr. 9, 315–336.

Van Cleve K and Zasada J 1976 Response of 70-year-old white spruce to thinning and fertilization in interior Alaska. Can. J. For. Res. 6, 145–152.

Van Cleve K, Oliver L, Schlentner R, Viereck L A and Dyrness C T 1983 Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. 13, 747–766.

Van Cleve K, Oechel W C and Hom J L 1990 Response of black spruce (*Picea mariana*) ecosystems to soil temperature modifications in interior Alaska. Can. J. For. Res. 20, 1530–1535.

Van Nostrand R S 1979 Growth response of black spruce in Newfoundland to N, P and K fertilization. For. Chron. 55, 189–193.

VEMAP Members 1995 Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochem. Cycles 9, 407–437.

Vukicevic T, Braswell B H and Schimel D S 2001 A diagnostic study of temperature controls on global terrestrial carbon exchange. Tellus 53B, 150–170.

Weber M G and Van Cleve K 1984 Nitrogen transformations in feather moss and forest floor layers of interior Alaska black spruce ecosystems. Can. J. For. Res. 14, 278–290.

Weetman G F 1975 Ten-year growth response of black spruce to thinning and fertilization treatments. Can. J. For. Res. 5, 302–309.

Xiao X, Melillo J M, Kicklighter D W, McGuire A D, Prinn R G, Wang C, Stone P H and Sokolov A P 1998 Transient climate change and net ecosystem production of the terrestrial biosphere. Global Biogeochem. Cycles 12, 345–360.