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

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## 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

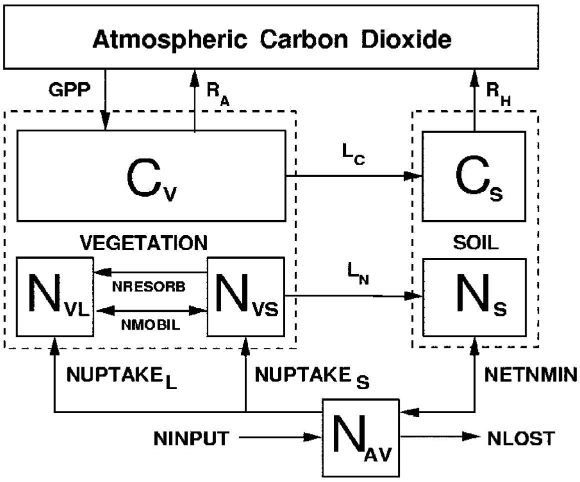

*Figure 1.* The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation ($C_V$); structural N in the vegetation ($N_{VS}$); labile N in the vegetation ($N_{VL}$); organic carbon in soils and detritus ($C_S$); organic N in soils and detritus ($N_S$); and available soil inorganic 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:

$$\begin{aligned}\mathrm{GPP} = {} & C_{\mathrm{max}} f(\mathrm{PAR})\, f(\mathrm{LEAF}) \\ & f(\mathrm{T})\, f(C_{\mathrm{a}}, G_{\mathrm{v}})\, f(\mathrm{NA}),\end{aligned}$$

where $C_{\mathrm{max}}$ 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, $C_{\mathrm{a}}$ is atmospheric $CO_2$ concentration, $G_{\mathrm{v}}$ is relative canopy conductance, and NA is N availability. The effects of elevated atmospheric $CO_2$ directly affect $f(C_{\mathrm{a}}, G_{\mathrm{v}})$ 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 $f(\mathrm{NA})$. 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, $f(\mathrm{NA})$ 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 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.

*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 |

## 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

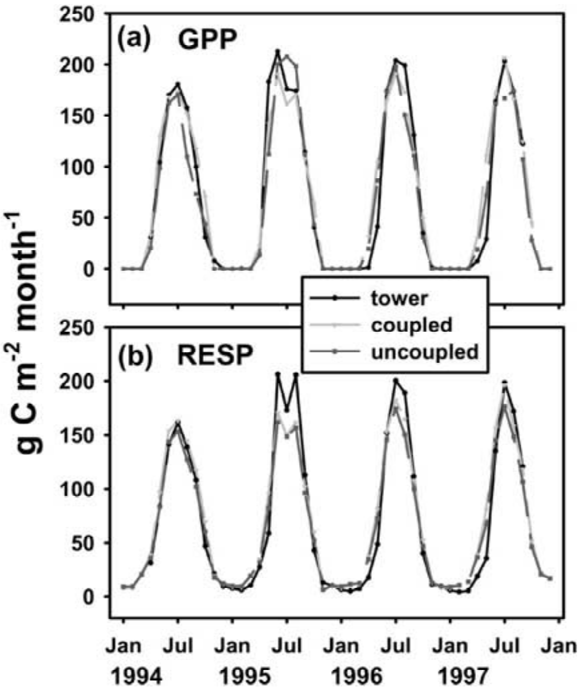

*Figure 2.* Field-based and simulated monthly variation in (a) gross primary production (GPP) and (b) total ecosystem respiration (RESP) for the northern site. Simulations were driven with local climate.

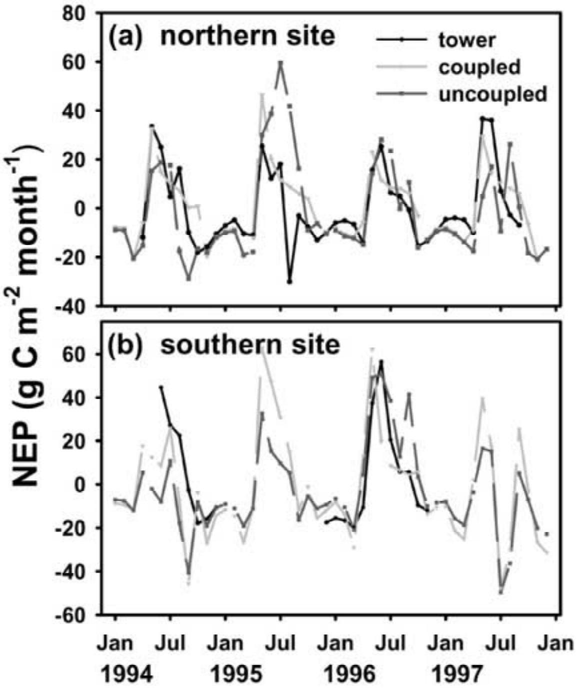

*Figure 3.* Field-based and simulated monthly variation in net ecosystem production (NEP) for (a) the northern site and (b) the southern site. Simulations were driven with local climate.

*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

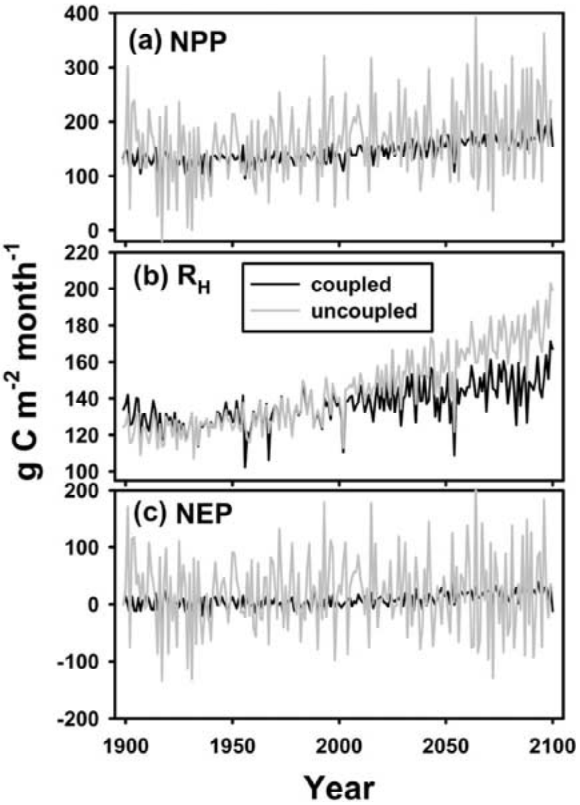

*Figure 4.* Historical and projected interannual variation in (a) net primary production (NPP), (b) heterotrophic respiration ($R_H$), and (c) net ecosystem production (NEP) for the northern site grid cell from the simulations by the coupled and uncoupled parameterizations of TEM.

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 variability 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.

| | | Historical period ($n$ = 94 years) | | | Projected period ($n$ = 106 years) | | |
|---|---|---|---|---|---|---|---|
| Parameterization | Flux | 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 | – |

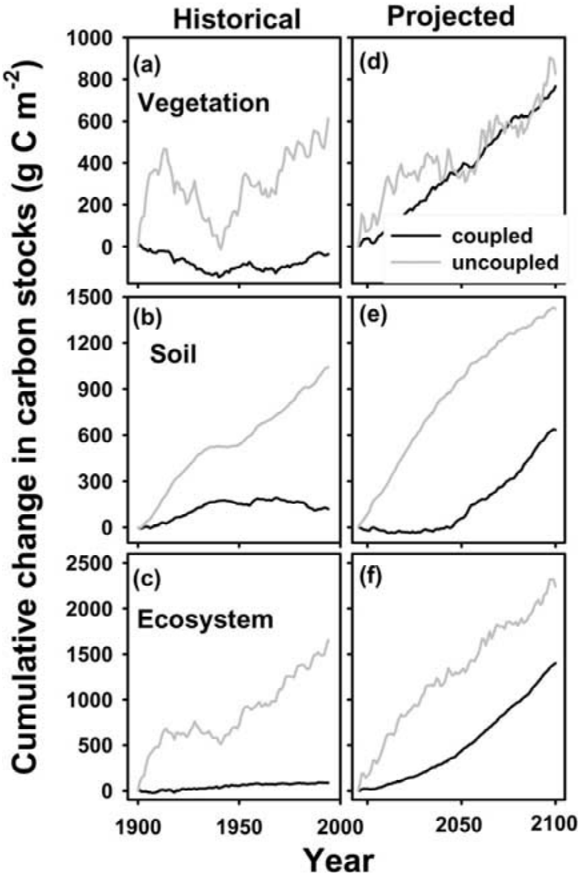

*Figure 5.* Historical and projected changes in (a,d) vegetation C, (b,e) soil C, and (c,f) ecosystem C for the northern site grid cell simulated by the coupled and uncoupled parameterizations of TEM. Changes in C stocks are expressed as the change in g m$^{-2}$ since 1900 for the historical period,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

*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 |

### *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

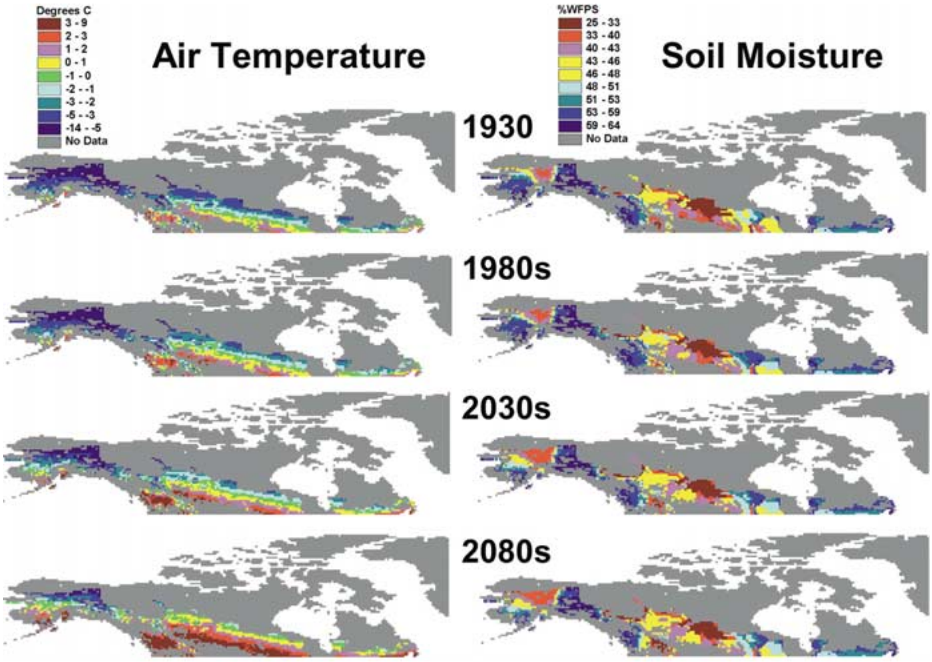

*Figure 6.* Spatial distribution of mean annual air temperature as °C and simulated mean annual soil moisture as percent water-filled pore space (%WFPS) across the range of North American black spruce ecosystems during four decades separated by 50 years during the simulation period 1900–2100: (a) 1930–1939, (b) 1980–1989, (c) 2030–2039, and (d) 2080–2089.

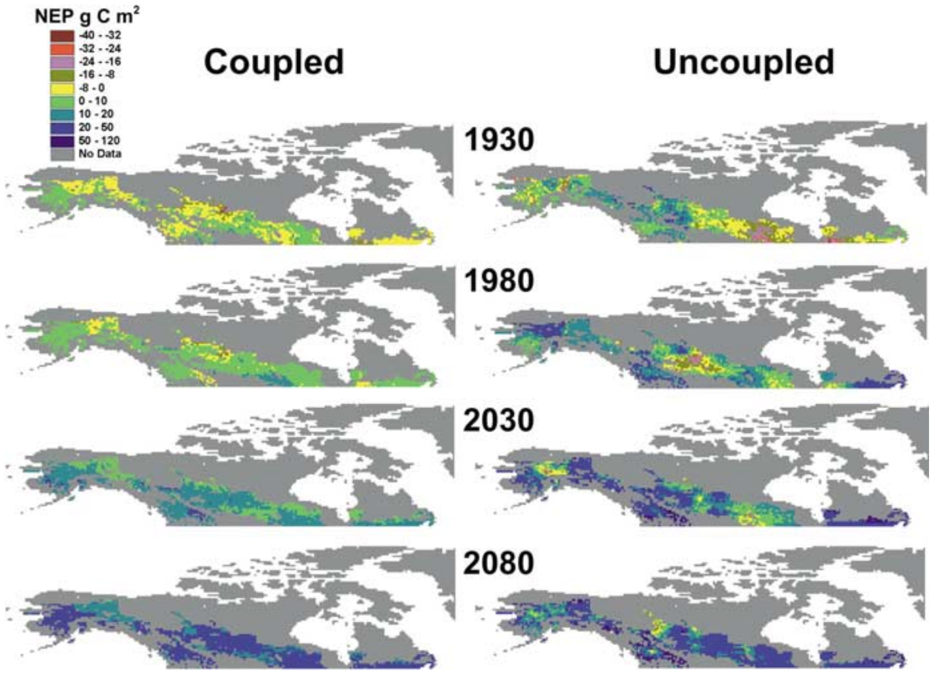

*Figure 7.* Simulated spatial and temporal variability in mean annual net ecosystem production (NEP) for the coupled and uncoupled parameterizations of TEM across the range of North American black spruce ecosystems during four decades separated by 50 years during the simulation period 1900–2100: (a) 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 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 $CO_2$.

*Table 6.* Proportion of variation explained by correlation of simulated mean annual net primary production (NPP) and heterotrophic respiration ($R_{\mathrm{H}}$) 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 | $< 0.10$ | $< 0.02$ | $< 0.10$ |
| | $R_{\mathrm{H}}$ | 0.36 | 0.13 | $< 0.10$ | 0.48 |
| 1980 – 1989 | NPP | 0.35 | 0.10 | $< 0.02$ | 0.10 |
| | $R_{\mathrm{H}}$ | 0.47 | 0.13 | $< 0.02$ | 0.45 |
| 2030 – 2039 | NPP | 0.27 | $< 0.10$ | $< 0.02$ | $< 0.10$ |
| | $R_{\mathrm{H}}$ | 0.45 | $< 0.10$ | $< 0.02$ | 0.47 |
| 2080 – 2089 | NPP | 0.31 | $< 0.10$ | $< 0.02$ | $< 0.10$ |
| | $R_{\mathrm{H}}$ | 0.42 | $< 0.10$ | $< 0.02$ | 0.46 |

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.

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