

Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century

M. S. BALSHI*, A. D. MCGUIRE, P. DUFFY, M. FLANNIGAN‡, D. W. KICKLIGHTER, and J. MELILLO ,

*Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK9775, USA, †U S Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK 99775, USA, ‡Neptune & Company, Lakewood, CO 80215, USA, §Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, ON P6A 2E5, USA, ¶Marine Biological Laboratory, The Ecosystems Center, Woods Hole, MA 02543, USA

Abstract

The boreal forest contains large reserves of carbon. Across this region, wildfires influence the temporal and spatial dynamics of carbon storage. In this study, we estimate fire emissions and changes in carbon storage for boreal North America over the 21st century. We use a gridded data set developed with a multivariate adaptive regression spline approach to determine how area burned varies each year with changing climatic and fuel moisture conditions. We apply the process-based Terrestrial Ecosystem Model to evaluate the role of future fire on the carbon dynamics of boreal North America in the context of changing atmospheric carbon dioxide (CO₂) concentration and climate in the A2 and B2 emissions scenarios of the CGCM2 global climate model. Relative to the last decade of the 20th century, decadal total carbon emissions from fire increase by 2.5–4.4 times by 2091–2100, depending on the climate scenario and assumptions about CO₂ fertilization. Larger fire emissions occur with warmer climates or if CO₂ fertilization is assumed to occur. Despite the increases in fire emissions, our simulations indicate that boreal North America will be a carbon sink over the 21st century if CO₂ fertilization is assumed to occur in the future. In contrast, simulations excluding CO₂ fertilization over the same period indicate that the region will change to a carbon source to the atmosphere, with the source being 2.1 times greater under the warmer A2 scenario than the B2 scenario. To improve estimates of wildfire on terrestrial carbon dynamics in boreal North America, future studies should incorporate the role of dynamic vegetation to represent more accurately post-fire successional processes, incorporate fire severity parameters that change in time and space, account for human influences through increased fire suppression, and integrate the role of other disturbances and their interactions with future fire regime.

Keywords: boreal carbon dynamics, climate change, fire emissions

Received 4 June 2008; revised version received 19 December 2008 and accepted 8 January 2009

Introduction

Relationships between climate and fire across the North American boreal region indicate a general increasing trend in the area burned historically (Gillett *et al.*, 2004; Kasischke & Turetsky, 2006). It is believed that these trends in area burned will continue into the future (Flannigan *et al.*, 1998, 2000; Stocks *et al.*, 1998; Balshi

et al., 2008). An altered fire regime in response to future climatic changes (Wotton & Flannigan, 1993; Flannigan *et al.*, 2000, 2005; Carcaillet *et al.*, 2001) has strong implications for the carbon dynamics of this region. Changes in the carbon emitted due to wildfire in response to changes in climate may act as a potentially strong positive feedback to atmospheric carbon dioxide (CO₂) concentrations (Kasischke *et al.*, 1995) as well as surface energy exchange (Chapin *et al.*, 2000; Chambers & Chapin, 2003; Amiro *et al.*, 2006; Randerson *et al.*, 2006). Wildfire shows a great deal of interannual variation in area burned and severity (Kasischke & Turetsky,

Correspondence: Michael S. Balshi, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK9775, USA, fax +1 907 474 7872, e-mail: mbalshi@neptuneinc.org

2006), which makes it difficult to predict the effect of wildfire on carbon storage for future scenarios of climate change.

Several studies have incorporated the influence of fire into process-based models, but the applications of these models have primarily been focused on retrospective analyses of carbon dynamics (Peng & Apps. 1999; Amiro *et al.*, 2000; Chen *et al.*, 2000, 2003; Thonicke *et al.*, 2001; Venevsky *et al.*, 2002; Hicke *et al.*, 2003; Balshi *et al.*, 2007). Relatively few studies have investigated the influence of future fire disturbance on the carbon dynamics of the North American boreal region in the context of a changing climate and atmospheric CO_2 concentrations. Zhuang *et al.* (2006) evaluated the role of fire in pan-boreal carbon dynamics assuming that area burned increases at a fixed rate of $1\% \text{ yr}^{-1}$ from 2000 to 2100. However, the assumption of a fixed rate of increase in area burned in the boreal forest is simplistic as wildfire tends to be episodic in nature, with some years experiencing larger, more catastrophic burn years than others (Murphy *et al.*, 2000; Kasischke *et al.*, 2002). Bachelet *et al.* (2005) used a dynamic global vegetation model to examine the influence of climate and fire on the carbon dynamics of Alaska. While the area burned in that study was allowed to vary from year to year based on the Palmer Drought Index, the influence of fire disturbance legacies, as represented by the evolution of stand-age distributions across the landscape, was not considered.

Balshi *et al.* (2008) developed spatially and temporally explicit empirical relationships for the North American boreal region that relate area burned with air temperature and the fuel moisture indices and monthly severity rating of the Canadian Fire Weather Index System. The advantage of this approach is that it captures the spatiotemporal variation in the influence of the model predictor variables across the boreal region in addition to incorporating the influence of fuel moisture for different depths of the ground layer. With the overall goal of examining the vulnerability of carbon storage in the North American boreal region to future fire, we build on the cohort approach developed by Balshi *et al.* (2007), and incorporate the role of the legacy of previous fire disturbances and a climatically driven future fire regime on the future carbon dynamics of North America north of 45°N (referred to hereafter as 'boreal North America'). The objectives of this study are to estimate future fire emissions and carbon storage of this region using estimates of future area burned (Balshi *et al.*, 2008), and to evaluate the carbon dynamics of the region in the context of ecosystem responses to changes in future atmospheric CO_2 concentration and changes in climate. We also identify sources of uncertainty that should be addressed in studies that estimate the role of future fire on the carbon dynamics of this region.

Methods

Overview

In this study, we use the process-based Terrestrial Ecosystem Model (TEM) to evaluate how changes in atmospheric CO_2 , climate, and fire disturbance over the 21st century influence carbon dynamics for the land-based area in North America north of 45°N . We use three steps to initialize our simulations for the state of these ecosystems at the beginning of the year 2003. First, we run the model to equilibrium [where annual net primary production (NPP) = annual heterotrophic respiration] for each 0.5° latitude $\times$ 0.5° longitude grid cell using long-term mean monthly climate from 1901 to 1930. Second, a 900-year spin-up is conducted to dynamically equilibrate the TEM to variability in climate using data describing the annual climate conditions for the period 1901–1930, repeatedly. Third, TEM is then run from 1901 to 2002 using monthly climate based on observations. A backcasting approach (Balshi *et al.*, 2007) is used to account for the influence of fire on carbon dynamics before the start of the historical fire record including the 900-year spin-up period.

For future conditions, there is much uncertainty as to how atmospheric CO_2 concentrations and climate may change (IPCC, 2001). In addition, the importance of CO_2 fertilization on carbon sequestration remains a controversial topic (e.g. Caspersen *et al.*, 2000; Oren *et al.*, 2001; Joos *et al.*, 2002; Hungate *et al.*, 2003; Luo *et al.*, 2004, 2006; Körner *et al.*, 2005; Long *et al.*, 2006; Reich *et al.*, 2006; Canadell *et al.*, 2007). For example, free air CO_2 enrichment (FACE) experiments within young loblolly pine stands at the Duke Forest, North Carolina have documented significant increases in vegetation carbon (DeLucia *et al.*, 1999; Allen *et al.*, 2000), litterfall (Allen *et al.*, 2000) and the accumulation of litter in soils (Schlesinger & Lichter, 2001) in response to elevated CO_2 . Other studies (e.g. Norby *et al.*, 1992; Lovelock *et al.*, 1998; Caspersen *et al.*, 2000) have indicated that elevated CO_2 has no or little effect on the accumulation of vegetation biomass. As FACE studies have not yet been conducted in the boreal forest, the issue of whether NPP of boreal forests will respond to elevated CO_2 is an uncertainty. To examine the consequences of these uncertainties on carbon dynamics in boreal North America, we conduct two sets of three simulations for each of two different climate scenarios (12 simulations in total) for the period 2003–2100. In the first set of simulations, we ran the model with a constant atmospheric concentration of CO_2 so that there was no response of gross primary production (GPP) to future changes in CO_2 (i.e. simulations without CO_2 fertilization) while in the second set we ran the model with increases in the future

concentrations of atmospheric CO₂ (i.e. simulations with CO₂ fertilization). For the set with CO₂ fertilization, we conduct three simulations. In simulation one (S1), atmospheric CO₂ concentrations vary, but a mean month [y climate is used from] 901-1930 to represent the climate for each year. Fire disturbance is not included in this simulation. In simulation two (S2), both atmospheric CO₂ concentrations and monthly climate vary, but disturbance by fire is excluded. In simulation three (S3), atmospheric CO₂ concentrations and monthly climate vary and fire disturbances are assumed to occur. For the set of simulations without CO₂ fertilization, we conduct the same three simulations as in the first set, but with atmospheric CO₂ fixed at 296 ppm, which is the mole fraction used to initialize each simulation. The changes in atmospheric CO₂ concentration and climate conditions are derived from output of the second generation of the Canadian Center for Climate Modeling and Analysis Coupled Global Climate Model (CGCM2) driven by either the A2 or B2 emissions scenarios of the IPCC Third Assessment (TPCC, 2001). Future fire disturbance for the period 2003-2100 is derived from an empirical modeling approach presented in Balshi *et al.* (2008) also using the CGCM2 output. We then analyze our simulation results for the North American region north of 45°N. The effect of CO₂ fertilization on carbon storage is determined by the results of simulation S1. The effect of climate on carbon storage is determined by the difference between simulations S2 and S1. The effect of fire on carbon storage, which includes the effects of fire emissions as well as changes in carbon storage associated with the stand-age structure of the region, is determined by the difference between the simulations S3 and S2.

Tile TEM

The TEM is a large-scale, process-based biogeochemical model that estimates monthly pools and fluxes of carbon and nitrogen for terrestrial ecosystems. TEM is driven by a series of spatially explicit data sets that include climate, elevation, soil texture, and vegetation. The equations and parameters of TEM have been documented in previous studies (Raich *et al.*, 1991; McGuire *et al.*, 1992; Tian *et al.*, 1999; Zhuang *et al.*, 2003; Euskirchen *et al.*, 2006; Balshi *et al.*, 2007) and the model has been applied to regions around the globe, including the high latitudes (McGuire *et al.*, 2000a, b, 2001, 2002, 2004; Clein *et al.*, 2000, 2002, 2007; Zhuang *et al.*, 2001, 2002, 2003, 2006; Euskirchen *et al.*, 2006, 2007; Balshi *et al.*, 2007). Several of the parameters in TEM are based on values obtained in the peer-reviewed literature. However, the rate-limiting parameters are defined by calibrating the model to pools and fluxes of field sites

that are representative of particular ecosystems. The model is coupled to a soil thermal model and can be applied on both permafrost and nonpermafrost soils. In this study we use TEM version 5.1 (Euskirchen *et al.*, 2006; Balshi *et al.*, 2007), which incorporates the effects of fire on both carbon and nitrogen dynamics. To estimate changes in carbon storage we calculate the net ecosystem carbon balance (NECB, Chapin *et al.*, 2006) for outputs generated by the model as

$$\text{NECB} = \text{NPP} - R_h - \text{TCE}, \quad (1)$$

where NPP is net primary production, R_h is heterotrophic respiration, and TCE is total carbon emitted due to fire [Eqn (1)]. Disturbances due to insects, land-use change, and forest harvest are not included in the calculation of NECB in this study.

The flux NPP is calculated as the difference between GPP (the CO₂ fixed by vegetation in photosynthesis) and autotrophic respiration (R_A , the respiration of CO₂ by vegetation). Monthly GPP considers the effects of several factors and is calculated as follows:

$$\text{GPP} = C_{\max} f(\text{PAR}) f(\text{PHENOLOGY}) f(\text{FOLIAGE}) f(T) f(C_a, G_v) f(\text{NA}) f(\text{FT}), \quad (2)$$

where $C_{\max}$ is the maximum rate of C assimilation, PAR is photosynthetically active radiation, $f(\text{PHENOLOGY})$ is monthly leaf area relative to maximum monthly leaf area (Raich *et al.*, 1991). The function $f(\text{FOLIAGE})$ is a scalar function that ranges from 0.0 to 1.0 and represents the ratio of canopy leaf biomass relative to maximum leaf biomass (Zhuang *et al.*, 2002), T is monthly air temperature, C_a is atmospheric CO₂ concentration, G_v is relative canopy conductance, and NA is nitrogen availability. The effects of elevated atmospheric CO₂ directly affect $f(C_a, G_v)$ by altering the intercellular CO₂ of the canopy (McGuire *et al.*, 1997; Pan *et al.*, 1998). The function $f(\text{NA})$ models the limiting effects of plant nitrogen status on GPP (McGuire *et al.*, 1992; McGuire *et al.*, 1997; Pan *et al.*, 1998; Sokolov *et al.*, 2008). The function $f(\text{FT})$ is an index of submonthly freeze-thaw, which represents the proportion of a specific month in the which the ground is thawed (Zhuang *et al.*, 2003; Euskirchen *et al.*, 2006).

The flux R_A is the sum of maintenance respiration (R_m) and growth respiration (R_g), which is prescribed to be 20% of the difference between GPP and R_m . The flux R_m is a direct function of plant biomass as follows:

$$R_m = K_r C_v e^{rT}, \quad (3)$$

where K_r is the per-gram-biomass respiration rate of the vegetation at 0°C, C_v is the vegetation carbon pool, T is the mean monthly air temperature, and r is the instantaneous rate of change in respiration with the change in temperature.

Table 1 Literature estimates of average aboveground (β_a) and ground layer (β_g) carbon fraction consumed used in the severity module of TEM for emissions estimates during a fire event for North America (French *et al.*, 2000)

Ecozone	Aboveground (β_a) C fraction consumed	Ground layer (β_g) C fraction consumed	Average area burned (ha)	Average emission (Tg C yr ⁻¹)	Average emission per m ² of burned area (g C m ² yr ⁻¹)
<i>North America</i>					
Alaska Boreal Interior	0.23	0.36	289 000	7.2	2470
Boreal Cordillera	0.13	0.38	1 59 000	5.7	3580
Taiga Plain	0.25	0.06	3 62 000	6.0	1650
West Taiga Shield	0.25	0.05	3 69 000	3.3	896
East Taiga Shield	0.25	0.05	1 41 000	2.1	1490
West Boreal Shield	0.26	0.06	5 31 000	15.2	2860
East Boreal Shield	0.22	0.06	95 000	0.2	256
Boreal Plain	0.24	0.11	2 27 000	7.8	3420
Hudson Plain	0.24	0.05	56 300	0.8	1430

Also shown are mean annual area burned, mean annual total carbon emission, and mean annual total carbon emission per square meter of burned area from model simulations of Balshi *et al.* (2007) for North America (1959–2002).

The flux R_h represents the decomposition of all organic matter and is calculated as follows:

$$R_h = K_d C_s e^{rsT} f(M), \quad (4)$$

where K_d is the per-gram-biomass respiration rate of soil organic matter at 0°C, C_s is soil carbon pool, T is the mean monthly air temperature, and rs is the instantaneous rate of change in decomposition with the change in temperature, and $f(M)$ is a scalar between 0 and 1 of volumetric soil moisture (M) effects on decomposition.

Our approach to modeling fire emissions (TCE) is based on calculating the total carbon emitted during a fire event from aboveground and ground layer carbon consumption estimates

$$TCE = (\beta_a \times V_c) + (\beta_g \times S_c), \quad (5)$$

where TCE is the total carbon emitted, B_g is the aboveground C fraction consumed, B_g is the ground layer carbon fraction consumed during a fire, V_c is vegetation carbon, and S_c is soil carbon. The parameters B_a and f which represent the effects of fire severity on carbon release during fire, vary spatially across boreal North America (Table 1) and are based on literature estimates of aboveground and ground layer carbon fraction consumed during a fire for different ecozones of boreal North America (see French *et al.*, 2000). Vegetation carbon consumed during fire events ranges from 13% to 26% depending on ecozone and soil carbon consumed during fire ranges from 5% to 38% depending on ecozone. For boreal North America, we assumed a fire regime that is predominantly stand replacing and specified that 1% of the preburn live plant biomass would be available for regeneration following a fire. The soil pool after a fire contains both the soil organic

matter that was not combusted and vegetation carbon that was killed but not combusted. Mean annual area burned, mean total fire emissions, and emissions per unit of burned area for different ecozones of North America over the historical fire record (1959–2002) from the simulations of Balshi *et al.* (2007) are also shown in Table 1.

Based on Harden *et al.* (2004) and Wirth *et al.* (2002), we assumed that 85% of soil and vegetation nitrogen potentially consumed by fire was retained in the form of soil inorganic nitrogen. The nitrogen lost from the ecosystem as a result of fire is reintroduced into the system annually in equal increments obtained by dividing the total net nitrogen lost to the atmosphere during the most recent fire event by the fire return interval of the grid cell; fire return interval data used in this study are based on those used in Balshi *et al.* (2007) for boreal North America. This allows nitrogen to be reintroduced into the system as the ecosystem fixes nitrogen from the atmosphere during postfire succession, and is meant to represent the net difference of inputs from nitrogen fixation and losses from nitrogen leaching. Total inorganic nitrogen availability after fire is thus affected by nitrogen retention after fire, inputs of inorganic nitrogen reintroduced into the system after fire, the gross mineralization of nitrogen from soil organic matter into the inorganic nitrogen pool, and the uptake of inorganic nitrogen by both microbes (immobilization) and plants. In general, inorganic nitrogen availability increases immediately after a fire primarily because of nitrogen retention and the much reduced uptake of inorganic nitrogen by the vegetation. Also, gross mineralization of nitrogen will generally decrease because of a decrease in soil organic nitrogen and nitrogen immobilization by

microbes will generally increase because of the increase in inorganic nitrogen pools, so that the net nitrogen mineralization (the difference between gross mineralization and immobilization) will decrease immediately after a fire. Through succession after fire inorganic nitrogen availability will dynamically change as both plant nitrogen uptake increases because of increasing vegetation biomass, gross mineralization increases because of an increase in organic nitrogen stocks, and immobilization responds to dynamic changes in inorganic nitrogen availability.

Input data sets

To extrapolate the TEM across boreal North America, we used driving data sets that have (1) only temporal variability (atmospheric CO₂ concentration), (2) only spatial variability (elevation, soil texture, and vegetation), and (3) both spatial and temporal variability (air temperature, precipitation, cloudiness, and fire disturbance). These data sets are described in more detail in the following sections.

Data used to initialize ecosystem state in year 2003. In this study, we simulated the response of carbon dynamics to historical atmospheric CO₂, climate, and fire using the same data sets and procedures as outlined in an earlier study by Balshi *et al.* (2007). Atmospheric CO₂ data were obtained from the Mauna Loa station (Keeling & Whorf, 2005). TERRAINBASE v1.1 elevation data were obtained from the National Geophysical Data Center, Boulder, CO (NGDC, 1994) and aggregated to a 0.5° spatial resolution. Soil texture, represented as percent silt plus percent clay in TEM, was based on the Global Gridded Surfaces of Selected Soil Characteristics data set (Global Soil Data Task Group/IGBP-DIS, 2000) and gridded at 0.5° spatial resolution. The input vegetation data set, gridded at 0.5° resolution, was represented by a potential natural vegetation map described by Melillo *et al.* (1993). Vegetation type remains static through time and does not accommodate biome shifts with changes in climate. The general parameterization of the model version used in this study is based on the parameterization of Euskirchen *et al.* (2006), and includes vegetation-specific parameters for polar desert, moist tundra, boreal forest, temperate conifer forest, temperate deciduous forest, and temperate grassland. A time-series data set of 0.5° gridded climate data was obtained from the Climate Research Unit (CRU) of the University of East Anglia (Mitchell & Jones, 2005) and used to prescribe historical climate from 1901 to 2002.

To represent the occurrence and distribution of historical fires (1959–2002 for Canada; 1950–2002 for

Alaska), we used the 0.5° gridded time series of fire disturbance developed by Balshi *et al.* (2007). With this data set, the legacies of past fire disturbances on carbon storage are determined by stratifying the vegetation in a 0.5° grid cell into cohorts of different stand ages. Each cohort is determined from one of several unique fire histories that may occur in the grid cell (for details, see Balshi *et al.*, 2007). The cohort information in year 2002 is then used to develop cohorts based on area burned for years 2003–2100 (see 'Accounting for future stand age').

Simulation of future carbon dynamics. For simulating future carbon dynamics, we used the same static data sets for elevation, soil texture, and vegetation that were used for initializing the ecosystem state in 2003. New data sets, however, were developed to represent future climate, atmospheric CO₂ concentrations and fire disturbance as described below.

Future climate. We derived monthly data for years 2003–2100 at 3.75° × 3.75° resolution for air temperature, precipitation, and downwelling shortwave radiation from CGCM2 (<http://www.cccm.d.bc.ec.gc.ca/data/cgcm2/cgcm2.shtml>). A detailed description of the CGCM2 can be found in Flato & Boer (2001). CGCM2 has been used to produce ensemble climate change projections using the IPCC Third Assessment A2 and B2 scenario storylines. The A2 and B2 emissions storylines are discussed in detail in the IPCC Special Report on Emissions Scenarios (SRES) (Nakicenovic & Swart, 2000). The emissions scenarios act as representations of the future development of radiatively active emissions and are based on assumptions about socioeconomic, demographic, and technological changes. These scenarios are then converted into greenhouse gas concentration equivalents that are used as driving variables for GCM projections. The A2 scenario represents a world where energy usage is high, economic, and technological development is slow, and population growth reaches 15 billion by year 2100. The B2 scenario represents a world where energy usage is lower than the A2, economies evolve more rapidly, environmental protection is greater, and population growth is slower than the A2 (10.4 billion by year 2100).

The near term warming effect (through the mid-21st century) for the A2 scenario is less than the B2 scenario due to the greater cooling effect resulting from higher sulfur dioxide emissions (IPCC, 2001). The temperature changes for the A2 and B2 scenarios cross about the mid-21st century, with the A2 scenario resulting in greater long-term warming due to higher emissions of radiatively active gases (IPCC, 2001).

We calculated anomalies between the contemporary climate means (1901–2002) relative to the A2 and B2

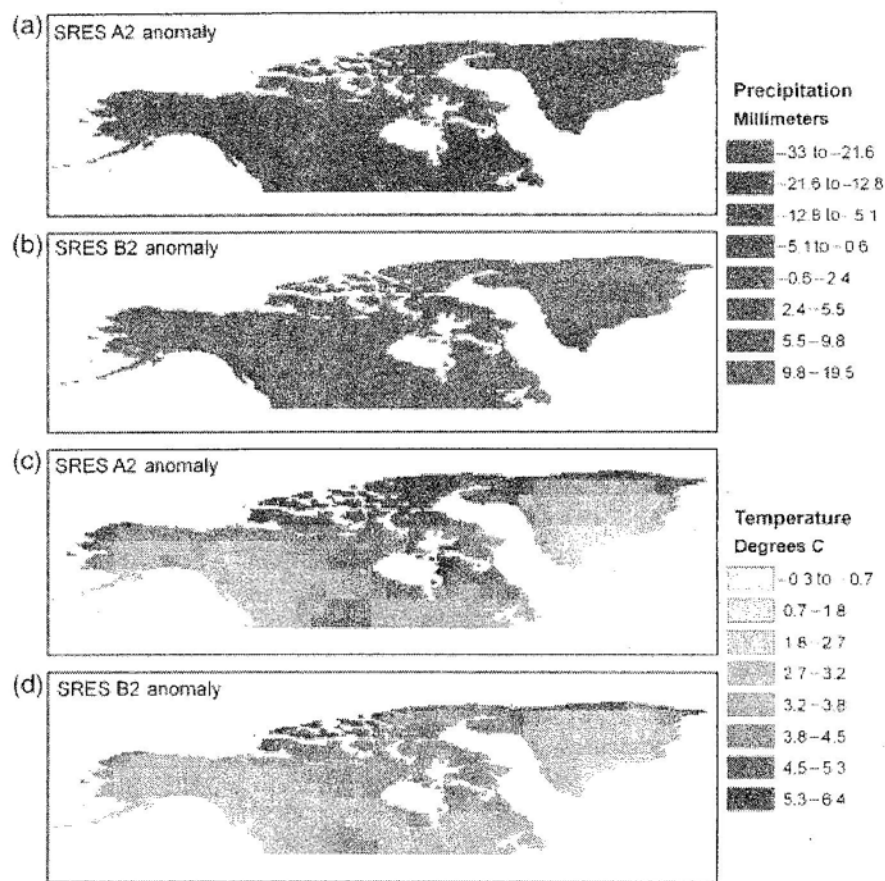


Fig. 1 Mean climate anomalies across the study region calculated for the period 2003–2100 (based on CGCM2 model output) relative to the 1901–2002 contemporary climate mean. Anomalies shown are averages for the (a) A2 scenario precipitation (mm), (b) B2 scenario precipitation (mm), (c) A2 scenario air temperature (°C), and (d) B2 scenario air temperature (°C).

climate means (2003–2100) to qualitatively assess the differences in temperature and precipitation change between the 20th and 21st Centuries (Fig. 1). Under an A2 scenario climate, precipitation anomalies indicate drier conditions in western Alaska through much of the interior and eastern regions across Canada relative to the B2 scenario (Fig. 1a and b). Similarly, temperature changes appear to be much greater under the A2 scenario and indicate warmer conditions across Alaska, western and central Canada to portions of Quebec and Labrador relative to the B2 scenario (Fig. 1c and d).

For simulations of ecosystem models driven by future climate, it is recommended that future changes from climate model simulations are superimposed on the present mean climate of the most reliable data sets of historical climate (Clein *et al.*, 2007; Rupp *et al.*, 2007; McCuire *et al.*, 2008). Both the CCCM2 A2 and B2 scenarios have a baseline period of 1961–1990 that corresponds to the IS92a scenario which is used to initialize the A2 and B2 scenarios for CCCM2. Because

we apply TEM at 0.5° spatial resolution in this study, these data were linearly interpolated across the simulation region. We then fused the CRU data to the CCCM2 scenarios by adjusting the CGCM2 monthly data relative to the absolute difference from the 1961–1990 CRU monthly mean by

$$\text{CGCM2}_{\text{adjusted monthly}} = \text{CRU}_\mu + (\text{CGCM2}_{\text{monthly}} - \text{CGCM2}_\mu), \quad (6)$$

in which CRU_μ is the mean monthly value for the period 1961–1990 derived from the CRU input data sets (described in 'Data used to initialize ecosystem state in year 2003'), $\text{CGCM2}_{\text{monthly}}$ is the monthly value output by CCCM2, and CGCM2_μ is the mean monthly value for the period 1961–1990 derived from the CCCM2 monthly data.

Future atmospheric CO_2 concentration. The equivalent CO_2 concentration used for simulating future climate by the CCCM2 includes climate forcing caused by

the atmospheric concentrations of other greenhouse gases (e.g. methane, nitrous oxide, ozone, etc.) in addition to CO₂. For simulations with TEM, we converted the CO₂ equivalent used to drive the CGCM2 into CO₂ concentration by developing relationships between the observed CO₂ record (Keeling & Whorf, 2005) and CO₂ equivalent concentrations for the period 1901–2000 using a series of regression models. The relationship between the observed CO₂ concentrations and CO₂ equivalent for the B2 scenario appeared to be linear ($R^2 = 0.99$; $P < 0.01$). However, the relationship between the observed CO₂ concentration and the A2 CO₂ equivalent was best described by a power model ($R^2 = 0.99$; $P < 0.01$). We then extrapolated atmospheric CO₂ concentration from year 2003 to 2100 using the empirical relationships developed for each scenario. These data sets were then appended to the observed atmospheric CO₂ record. The atmospheric CO₂ concentrations derived by the empirical relationships were greater under the A2 scenario (1100 ppm) than the B2 scenario (766 ppm) by the end of the 21st century.

Future fire disturbance data sets. To represent the area burned by future fires for the years 2003–2100, we used the 2.5° gridded data developed by Balshi *et al.* (2008) from models based on a multivariate adaptive regression spline (MARS) approach. MARS does not require that assumptions be made about the form of the relationship between the independent and dependent variables. Consequently, it can identify patterns and relationships that are difficult, if not impossible, for other regression methods to reveal. Briefly, our application of MARS to the study region involved the development of 127 independent models at 2.5° spatial resolution (total of 127 boreal cells across Alaska and Canada). The total number of models developed depended on the spatial and temporal coverage of historical fire records across the North American boreal region. The parameterization approach was designed to capture variation in the influence of predictor variables across the spatial extent of our domain (e.g. Alaska to Eastern Canada). The response variable is annual area burned and the predictor variables are monthly (April–September) air temperature and the monthly fuel moisture codes and severity rating of the Canadian Fire Weather Index System, for a total of 30 possible predictor variables for each grid cell (6 months $\times$ five predictors: air temperature, fine fuel moisture code, drought code, duff moisture code, and monthly severity rating). Climate and fire weather index system predictors were derived from the NCEP Reanalysis I project (Kalnay *et al.*, 1996) at 2.5° spatial resolution. Models were only developed for cells where the number of fire years (i.e. years where area burned is non-zero) in a given 2.5° cell is > 10 . We assumed all fires

were the result of lightning ignition as several studies have identified that most of the area burned in boreal North America is associated with lightning-caused fires (Kasischke *et al.*, 2002, 2006; Stocks *et al.*, 2002; Calef *et al.*, 2008).

We then evaluated the performance of the fire disturbance models by comparing predictions with observations over the period 1960–2002 across the study region. Model performance was validated against independent data for years 2003–2005 across Alaska and Canada. Following model development, we used climate model output from the CGCM2 to calculate fuel moisture codes for the period 2006–2100 based on the IPCC Third Assessment (IPCC, 2001). The fire models were then extrapolated for the period 2003–2100 using the SRES A2 and B2 scenario output from CGCM2. Predicted area burned between the A2 and B2 scenarios is similar through 2050, but diverges for the last 50 years of the 21st century, with the A2 scenario resulting in greater area burned (Fig. 2). Relative to the 1991–2000 baseline period defined by Balshi *et al.* (in press), area burned increases by 5.7 times under the A2 scenario while it increases by 3.5 times under the B2 scenario by the last decade of the 21st century.

Accounting for future stand age. We developed an algorithm to downscale the annual area burned estimates from 2.5° to 0.5° resolution by evenly distributing the future area burned estimates to land-based areas that are assumed to burn. Similar to the approach by Balshi *et al.* (2007), we account for differences in stand age resulting from multiple fires within a 0.5° grid cell. We distributed the burn area assigned to each 0.5° grid cell to existing cohorts that were created from the

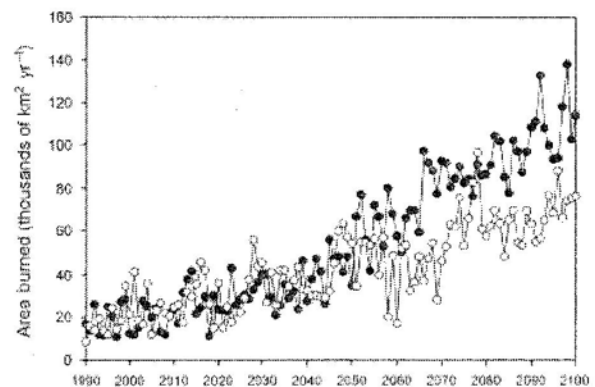


Fig. 2 Predicted annual area burned (thousands of km² yr⁻¹) driven by using NCEP model development data sets ('Observed'; 1990–2005) and the CGCM2 A2 and B2 Scenarios (2006–2100) from Balshi *et al.* (2008) for Alaska and western Canada. Dark circles represent the estimates driven by the A2 scenario while the open circle represent the estimate driven by B2 scenario.

historical fire data, starting with the oldest, until all existing cohorts burn. The logic underlying this approach assumes that older stands are more susceptible to burning than newly burned/regenerating stands. New cohorts were created if the burn area in a given year was either smaller or larger than the size of an existing cohort. Burned areas were only distributed to land-based areas within a given 0.5° grid cell containing vegetation types assumed to be burnable (e.g. boreal forest vs. ice/rock).

Results

We first present estimates of fire emissions across the North American boreal region and subregions. Boreal North American and subregional carbon dynamics of the 21st century are then evaluated with respect to the relative importance of atmospheric CO_2 , climate, and fire.

Future fire emissions

Mean annual decadal emissions increase from the beginning to the end of the 21st century, but vary with climate and CO_2 fertilization assumptions (Fig. 3) and are highly correlated with the mean annual decadal area burned (A2 and B2 scenario R^2 values = 0.97; $P < 0.0001$). For both climate scenarios, the simulations excluding CO_2 fertilization resulted in lower increases in fire emissions across all decades (Fig. 3b). The greatest differences between the simulations incorporating and excluding CO_2 fertilization are seen in the last 50 years of the 21st century. The larger emissions from fire for the simulations incorporating atmospheric CO_2 fertilization over this period is due to the greater amount of carbon sequestered during the first 50 years of the 21st century and therefore more biomass available for burning. Relative to the last decade of the 20th century, mean annual decadal emissions for the simulations that both included and excluded CO_2 (results reported as a range) under the A2 scenario increase 2.2–2.4 times by 2050 and 3.1–4.4 times by 2091–2100 (Fig. 3a and b). Mean annual decadal emissions for the simulations that both included and excluded CO_2 (results reported as a range) for the B2 simulations, increase 2.1–2.3 times by 2050 and 2.5–3.1 times by 2091–2100 (Fig. 3a and b). Mean annual decadal emissions are similar among climate scenarios for the first half of the 21st century but are greater for the A2 scenario in the last 50 years as a result of greater area burned (see Fig. 2).

21st century carbon dynamics for Boreal North America, 2003–2100

For the period 2003–2100, our simulations that considered the effect of atmospheric CO_2 fertilization on

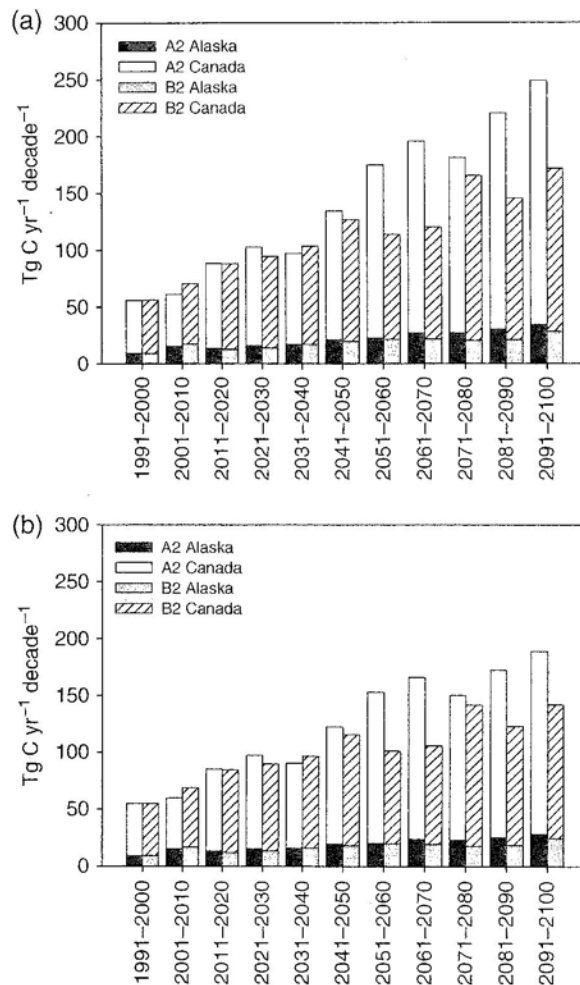


Fig. 3 Mean decadal total carbon emissions resulting from fire for boreal North America during the 21st century that (a) incorporate the effect of atmospheric CO_2 on photosynthesis and (b) exclude the role of atmospheric CO_2 fertilization on photosynthesis. The decade 1991–2000 is used as a comparison period and corresponds to years where fire emissions are driven by historical fire records. Units are $\text{Tg C yr}^{-1} \text{ decade}^{-1}$.

photosynthesis estimate that boreal North America is a carbon sink of 235.6 TgCyr^{-1} ($19.6 \text{ gCm}^{-2} \text{ yr}^{-1}$) and 178.5 TgCyr^{-1} ($14.8 \text{ gCm}^{-2} \text{ yr}^{-1}$) for the A2 and B2 scenarios, respectively (Table 2). The effects of CO_2 fertilization and climate acted to sequester carbon, while fire acted to release carbon to the atmosphere. For the warmer A2 scenario, CO_2 fertilization is responsible for sequestering carbon at a rate of 245.1 TgCyr^{-1} ($20.5 \text{ gCm}^{-2} \text{ yr}^{-1}$) while climate is responsible for sequestering 176.1 TgCyr^{-1} ($14.7 \text{ gCm}^{-2} \text{ yr}^{-1}$). For the B2 scenario, we estimate that CO_2 fertilization is responsible for sequestering approximately 30% less carbon (171.5 TgCyr^{-1} , or $14.3 \text{ gCm}^{-2} \text{ yr}^{-1}$) while climate is

Table 2 Mean annual changes in carbon storage for boreal North America from 2003 to 2100* driven by SRES A2 and B2 scenarios output by CGCM2

		Effects			
Scenario	Region	CO ₂	Climate	Fire	Total
<i>With CO₂ fertilization</i>					
A2	North America	245.1	176.1	-185.6	235.6
	Alaska	26.7	21.5	-12.0	36.2
	Canada	218.4	154.6	-173.7	199.3
B2	North America	171.5	147.0	-140.0	178.5
	Alaska	18.4	14.9	-9.4	23.9
	Canada	153.1	132.2	-130.6	154.7
<i>Without CO₂ fertilization</i>					
A2	North America	0.0	74.7	-139.4	-64.7
	Alaska	0.0	16.9	-11.0	5.9
	Canada	0.0	57.7	-128.4	-70.7
B2	North America	0.0	76.8	-106.8	-30.0
	Alaska	0.0	12.6	-8.3	4.3
	Canada	0.0	64.2	-98.5	-34.3

*Units are in Tg C yr⁻¹. Positive values indicate carbon sequestration by terrestrial ecosystems. Negative values indicate a release of carbon from land to atmosphere.

responsible for sequestering approximately 16% less carbon (147.0 Tg C yr⁻¹ or 12.3 g C m⁻² yr⁻¹), relative to the A2 scenario. The role of fire on carbon storage results in a source to the atmosphere at a rate of 185.6 Tg C yr⁻¹ (15.6 g C m⁻² yr⁻¹) and 140.0 Tg C yr⁻¹ (11.8 g C m⁻² yr⁻¹) for the A2 and B2 scenarios, respectively. Greater carbon is released to the atmosphere under the A2 scenario than the B2 scenario due to more area burned throughout the latter half of the 21st century.

The simulations that exclude the effect of CO₂ fertilization estimate a carbon source to the atmosphere of 64.7 Tg C yr⁻¹ (5.5 g C m⁻² yr⁻¹) and 30.0 Tg C yr⁻¹ (2.6 g C m⁻² yr⁻¹) for the A2 and B2 scenarios, respectively (Table 2). Alaska remains an overall carbon sink, while Canada becomes a carbon source to the atmosphere (Table 2). The effect of climate on carbon storage is similar among the A2 and B2 scenarios. Climate is responsible for a carbon sink of 74.7 Tg C yr⁻¹ (6.2 g C m⁻² yr⁻¹) and 76.8 Tg C yr⁻¹ (6.4 g C m⁻² yr⁻¹) for the A2 and B2 scenarios, respectively (Table 2). Fire, however, was responsible for releasing carbon to the atmosphere at a rate of 139.4 Tg C yr⁻¹ (1.7 g C m⁻² yr⁻¹) and 106.8 Tg C yr⁻¹ (9.0 g C m⁻² yr⁻¹) for the A2 and B2 scenarios, respectively (Table 2). Similar to the simulations incorporating atmospheric CO₂ fertilization, the A2 scenario resulted in greater area burned over the latter half of the 21st century and therefore resulted in greater carbon release to the atmosphere.

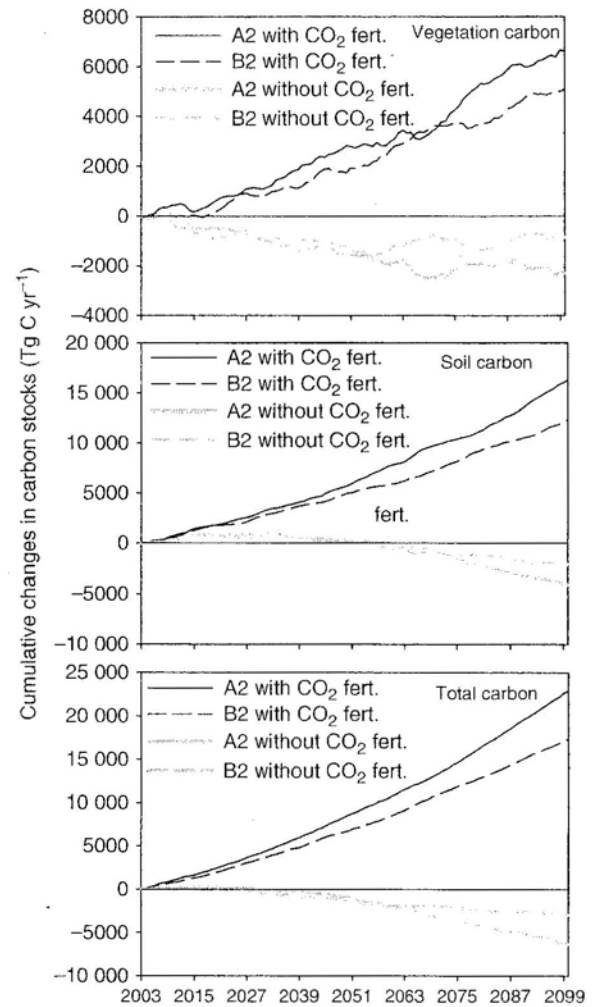


Fig. 4 Cumulative changes in vegetation, soil, and total ecosystem carbon stocks for North America from 2003 to 2100. Units are Tg C yr⁻¹. fert., fertilization.

We analyzed the cumulative changes in carbon stocks for vegetation, soil, and total ecosystem carbon pools in response to CO₂, climate, and fire for the period 2003–2100 (Fig. 4). For the simulations that included atmospheric CO₂ fertilization, vegetation carbon stocks increase throughout the 21st century, and are 24% greater for the A2 than B2 scenario by 2100 (Fig. 4). For the A2 scenario, vegetation carbon stocks show greater change in the last 35 years of the 21st century in comparison to the same period for the B2 scenario. Similar to the changes in vegetation carbon stocks, changes in soil carbon stocks result in approximately 25% greater carbon storage for the A2 scenario than for the B2 scenario (Fig. 4). By the end of the 21st century, we estimate that the cumulative changes in total carbon stored, relative to year 2003 is 22930 and 17370 TgC for the A2 and B2 scenarios, respectively. Thus, the warmer

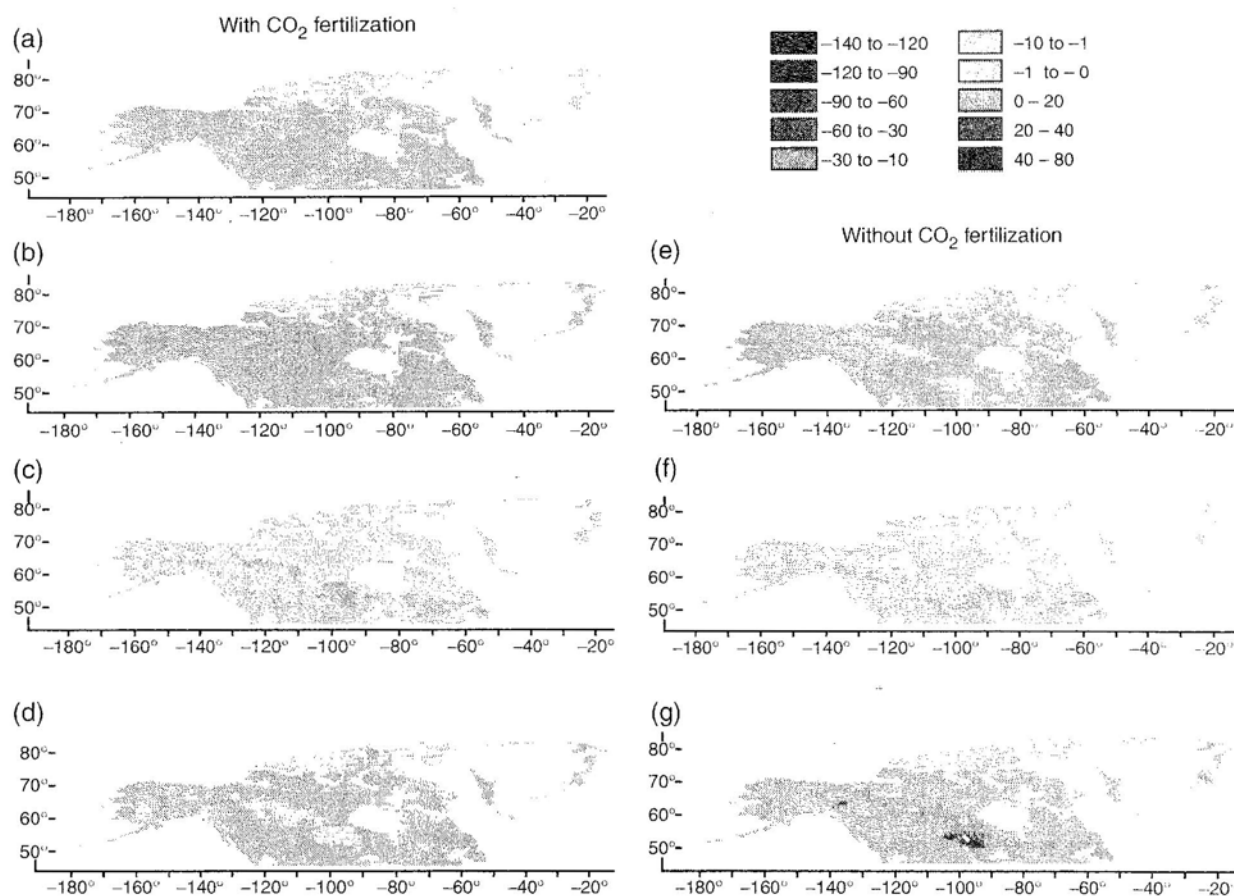


Fig. 5 Simulated mean annual net ecosystem carbon balance ($\text{g C m}^{-2} \text{yr}^{-1}$) of boreal North America estimated under the A2 climate scenario from 2003 to 2100 in response to (a) CO_2 fertilization, (b, e) climate, (c, f) fire, and (d, g) the combination of CO_2 , climate, and fire. Results are presented with and without a CO_2 fertilization effect on photosynthesis. Positive values represent carbon sequestration while negative values represent release of carbon from the land to the atmosphere.

scenario results in 24% greater carbon storage over the 21st century. For the simulations that exclude CO_2 changes in vegetation carbon stocks result in a carbon source for much of the 21st century (Fig. 4). The trend of changes in vegetation carbon stocks is similar among the A2 and B2 scenarios until 2060, but the A2 scenario results in greater release of carbon than the B2 scenario from 2061 to 2100 due to greater area burned (Fig. 4). Changes in soil carbon stocks shift from a carbon sink to a carbon source for this period for both climate scenarios, and are greater for the A2 scenario due to greater area burned over this period (Fig. 3). Changes in the vegetation carbon stocks for the first 60 years of the 21st century are responsible for the small total ecosystem carbon losses during this period, while in the last 40 years, vegetation and soil carbon are about equally important in promoting total carbon release to the atmosphere. Total carbon release to the atmosphere is

54% greater for the warmer A2 scenario by the end of the century (Fig. 4).

In addition to temporal variations in carbon storage, the ability of terrestrial ecosystems to sequester carbon varies across boreal North America (Figs 5 and 6). These spatial variations in carbon flux between the land and atmosphere also depend upon the assumptions made about CO_2 fertilization and climate change. Atmospheric CO_2 has a positive effect on carbon storage across boreal North America for the A2 (Fig. 5a) and B2 (Fig. 6a) scenarios. The effect of climate, however, shows both carbon sequestration and release to the atmosphere for the A2 (Fig. 5b) and B2 (Fig. 6b) climate scenarios. Carbon release is greater for the simulations that excluded CO_2 fertilization and is most evident in the islands north of the Canadian mainland, the MacKenzie mountain range, and portions of central Canada extending northeast to Hudson Bay (Figs 5e and 6e).

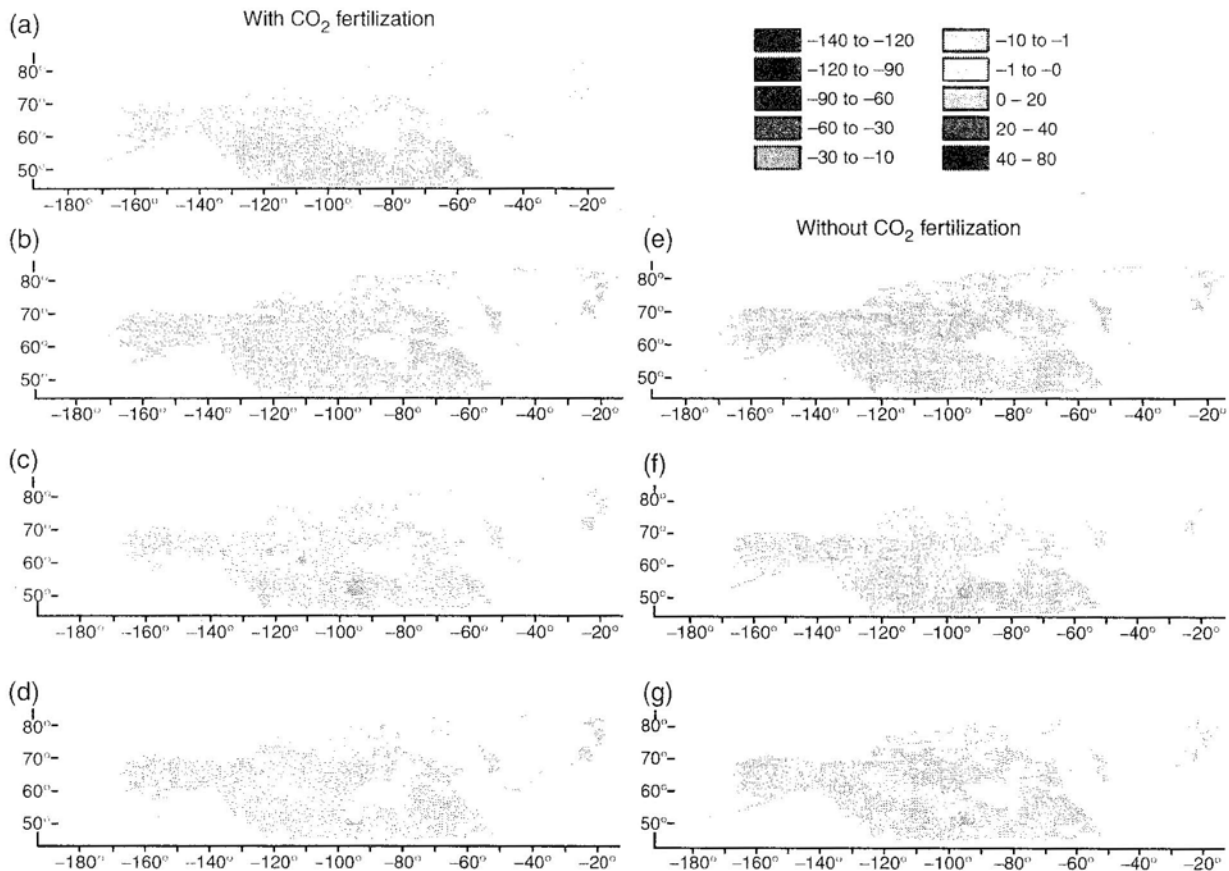


Fig. 6 Simulated mean annual net ecosystem carbon balance ($\text{g C m}^{-2} \text{yr}^{-1}$) of boreal North America estimated under the B2 climate scenario from 2003 to 2100 in response to (a) CO_2 fertilization, (b, e) climate, (c, f) fire, and (d, g) the combination of CO_2 , climate, and fire. Results are presented with and without a CO_2 fertilization effect on photosynthesis. Positive values represent carbon sequestration while negative values represent release of carbon from the land to the atmosphere.

These areas show the greatest effect of fire on NECB, which coincide with the regions where historical fire records and future fire estimates are concentrated. Carbon losses resulting from fire for the simulations that included a CO_2 fertilization effect are observed in portions of interior Alaska, extending through western and central Canada to portions of Labrador and Newfoundland, with greater losses under the A2 scenario (Fig. 5c) than the B2 scenario (Fig. 6c). Carbon losses resulting from fire for the simulations that excluded CO_2 fertilization were lower in comparison with the simulations that included a CO_2 fertilization effect on photosynthesis (Figs 5f and 6f). Greater carbon losses resulting from fire for the simulations that included CO_2 fertilization are due to greater total ecosystem carbon stocks resulting from the fertilization effect and therefore more biomass for burning (Table 2). The spatial extent of carbon losses is also different for the simulations excluding CO_2 fertilization. Under both climate scenarios, carbon losses resulting from fire are observed

in portions of interior Alaska, extending southeast through western and central Canada to portions of central Quebec (Figs 5f and 6f). Thus, although boreal North America acts overall as a carbon sink in response to the combined effect of CO_2 , climate, and fire for both climate scenarios (Table 2), there are regions which act as a carbon source, particularly where fires occurred and in regions that showed losses in response to climatic variability (Figs 5d and 6d). Similarly, in the simulations that excluded CO_2 fertilization, boreal North America acts overall as a carbon source to the atmosphere in response to climatic variability and fire (Table 2), but there are regions which still act as carbon sinks of atmospheric CO_2 (Figs 5g and 6g).

Decadal-scale carbon dynamics of the 21st century

To better understand temporal changes in the relative roles of CO_2 , climate, and fire effects on carbon dynamics across boreal North America over the 21st century, we calculated

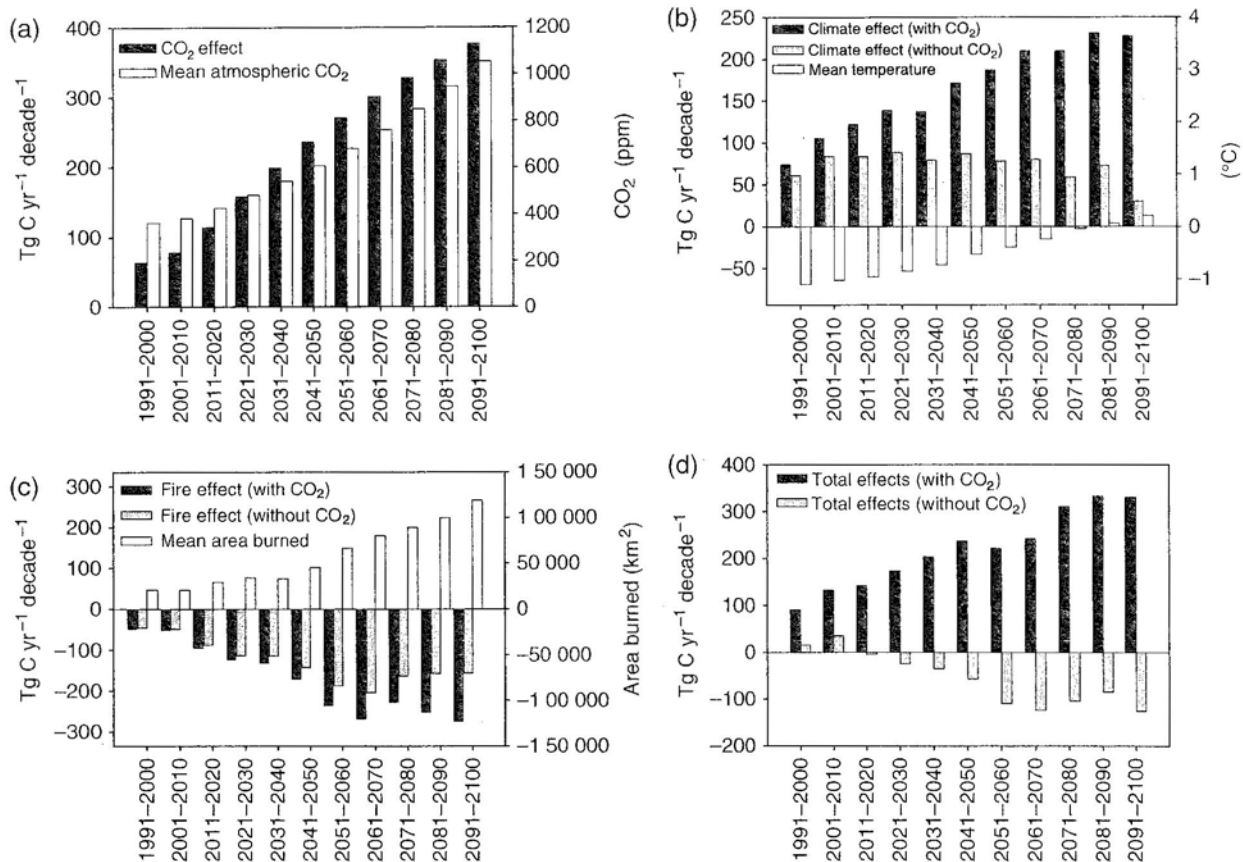


Fig. 7 Mean decadal effects from the A2 scenario simulations of (a) CO₂, (b) climate, (c) fire, and (d) the combined effects of CO₂, climate, and fire on simulated net ecosystem carbon balance for boreal North America for the 21st century. Also included is the period 1991–2000, which is used as a baseline comparison period. Each effect is compared with model driving data of mean decadal atmospheric CO₂ concentration, mean decadal air temperature, and mean decadal area burned across boreal North America. Positive values represent carbon sequestration by terrestrial ecosystems, while negative values represent a release of carbon from the land to the atmosphere.

mean decadal changes in carbon storage for the A2 (Fig. 7) and B2 (Fig. 8) simulations. For the A2 scenario, carbon storage increases each decade in response to increasing atmospheric CO₂ concentration (Fig. 7a). A similar pattern is observed for the B2 scenario; however, the effect of increasing carbon storage tends to plateau after 2061–2070 due to the deceleration of increasing atmospheric CO₂ concentration (Fig. 8a). The effect of increasing air temperature on carbon storage is similar for the A2 (Fig. 7b) and B2 (Fig. 8b) scenarios for the simulations incorporating CO₂ fertilization, with warmer mean temperatures promoting more carbon sequestration. In contrast, the set of simulations excluding atmospheric CO₂ fertilization shows that warming temperatures result in carbon sequestration that is relatively unchanged from decade to decade for the A2 (Fig. 7b) and B2 (Fig. 8b) scenarios, however, the last four decades do appear to become more variable which coincide with the warmest average decadal temperatures of the 21st century,

The effect of fire on decadal scale carbon dynamics shows that as area burned increases, fire generally releases more carbon to the atmosphere, with more carbon released per decade under the A2 climate scenario (Fig. 7c). Despite greater area burned for the period 2071–2080, relative to the previous decade, fire results in less of a carbon source for the simulations that both incorporate and exclude CO₂ fertilization (Fig. 7c). For the set of simulations excluding CO₂ fertilization, the last three decades that correspond to the greatest area burned, result in a carbon source that is relatively unchanged (Fig. 7c), while the carbon source increases from decade to decade for the set of simulations incorporating atmospheric CO₂ fertilization (Fig. 7c). The B2 scenario shows that as area burned increases through 2050, carbon released to the atmosphere also increases in simulations incorporating CO₂ fertilization (Fig. 8c). Future area burned under the B2 scenario then plateaus from 2041 to 2070 due to the relationship

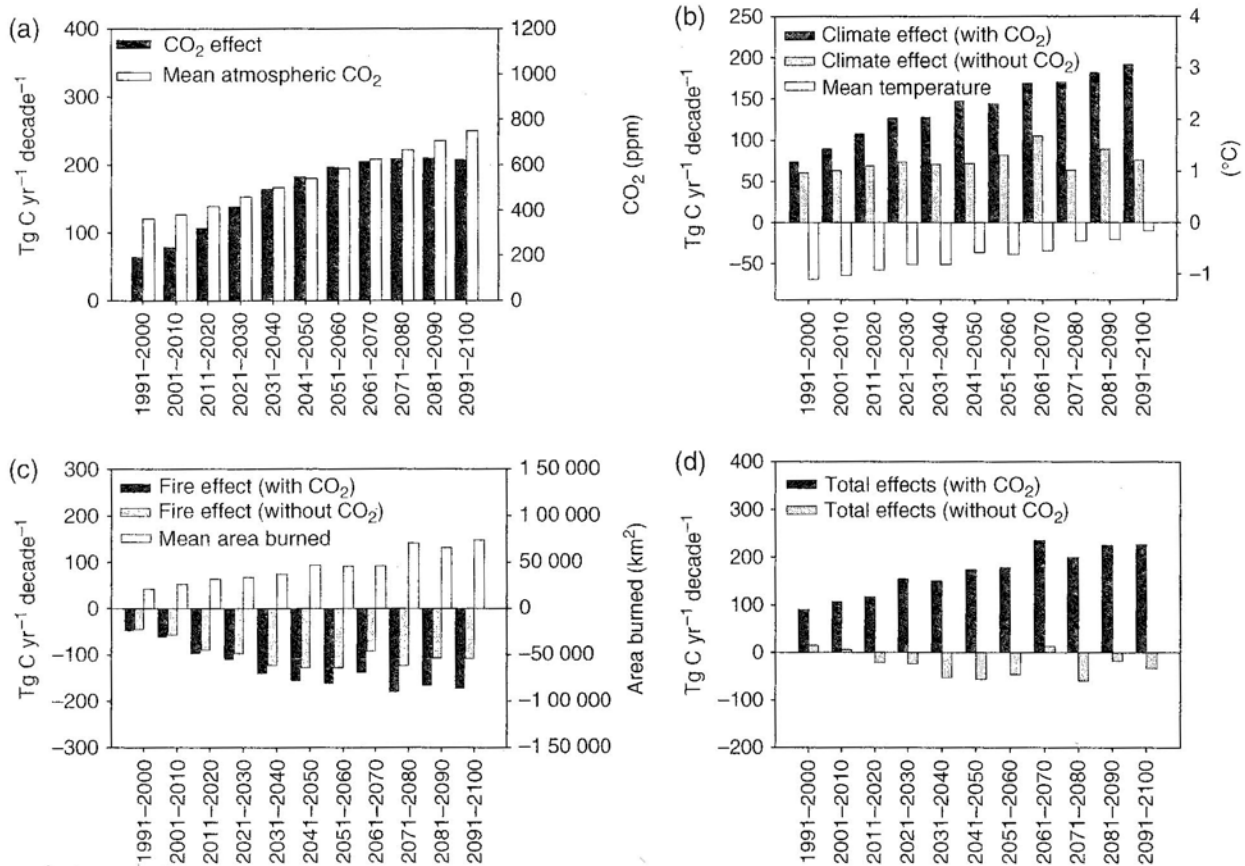


Fig. 8 Mean decadal effects from the B2 scenario simulations of (a) CO₂, (b) climate, (c) fire, and (d) the combined effects of CO₂, climate, and fire on simulated net ecosystem carbon balance for boreal North America for the 21st century. Also included is the last decade of the 20th century for reference. Each effect is compared with model driving data of mean decadal atmospheric CO₂ concentration, mean decadal air temperature, and mean decadal area burned across boreal North America. Positive values represent carbon sequestration by terrestrial ecosystems, while negative values represent a release of carbon from the land to the atmosphere.

between air temperature and fuel moisture indices on area burned (Fig. 2). The last three decades of the 21st century correspond to greater area burned under the B2 scenario and the effect of fire results in a larger carbon source to the atmosphere than the previous 70 years (Fig. 8c) due to greater fire emissions (Fig. 3a).

The combined effects of CO₂, climate, and fire on decadal scale carbon dynamics indicate that boreal North America is a carbon sink for the A2 (Fig. 7d) and the B2 (Fig. 8d) scenarios for the set of simulations incorporating atmospheric CO₂ as NPP is increasing faster than R_h and TCE (Fig. 9a and b). The last three decades under the A2 scenario show that the net carbon sink flux approximately triples relative to the period 1991-2000 (Fig. 7d). For the B2 scenario, the last four decades of the 21st century show that the carbon sink flux is more than double that of the period 1991-2000 (Fig. 8d). NPP, R_h and TCE increased faster under the A2 scenario (Fig. 9a) throughout the 21st century than under the B2 scenario (Fig. 9b). The set of simulations

excluding atmospheric CO₂ fertilization indicate that boreal North America is a small carbon sink in the first decade of the 21st century and becomes a carbon source in the remaining decades for the A2 scenario (Fig. 7d) as R_h and TCE increase faster than NPP (Fig. 9c). For the B2 scenario, North America is a small carbon source from 2011 to 2100 except for a small sink in 2061-2070 (Fig. 7d), which is a decade where NPP increased and R_h and TCE decreased relative to the previous decade (Fig. 9d).

Discussion

Effect of future climate change on Boreal North American fire emissions

In this study, we estimated the effects of two climate scenarios on boreal North American fire emissions, both including and excluding the effects of CO₂ fertilization on photosynthesis. The simulations suggest that climate

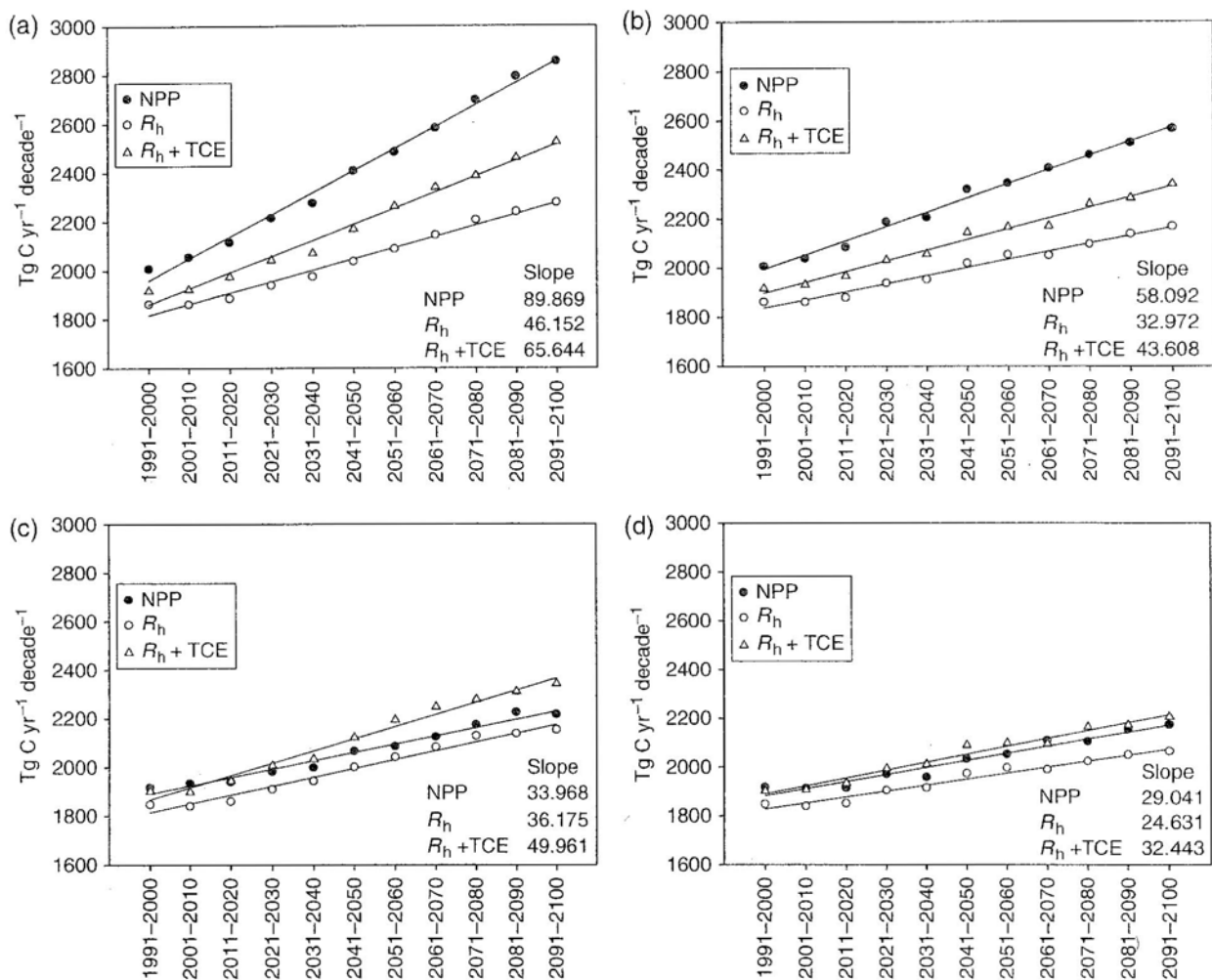


Fig. 9 Mean decadal net primary production (NPP), heterotrophic respiration (R_h), and the combination of heterotrophic respiration and fire emissions ($R_h + TCE$) in response to CO_2 , climate, and fire for the (a) A2 and (b) B2 scenarios incorporating the effect of atmospheric CO_2 fertilization and the (c) A2 and (d) B2 scenarios excluding the effect of atmospheric CO_2 fertilization on photosynthesis. Units are $Tg\ C\ yr^{-1}\ decade^{-1}$.

warming throughout the 21st century will, on average, result in greater levels of total carbon emitted by future wildfires. Our estimates suggest that by the end of the 21st century (2091–2100), total carbon emitted by wildfire is between 25% and 30% higher under the A2 scenario than the B2 scenario and the higher emissions are the result of greater area burned (Fig. 2). The A2 and B2 simulations that exclude the effect of CO_2 fertilization on photosynthesis result in lower total carbon emissions for each decade than the corresponding simulations including the effect of CO_2 fertilization. The effect of CO_2 fertilization results in greater carbon sequestration for that set of simulations and therefore greater carbon emitted at the time of fire due to greater biomass available for burning (Fig. 4). Balshi *et al.* (2007) reported minor differences in total carbon emission

estimates for the period 1959–2002 for simulations including and excluding CO_2 fertilization on photosynthesis. Our results suggest that CO_2 fertilization plays a much larger role in the emissions resulting from future area burned.

Bachelet *et al.* (2005) used a dynamic vegetation model that simulates the effects of fire to estimate the role of fire on carbon dynamics for Alaska through year 2100. They report an average loss of 17–19 $Tg\ C\ yr^{-1}$ due to fire emissions for the period 2025–2099 based on simulations with two climate scenarios. Our simulations estimate a range of between 18 and 25 $Tg\ C\ yr^{-1}$ emitted at the time of fire for Alaska over the same period. The larger range of emissions estimates from our study can be attributed to greater future area burned estimates for the period 2051–2090 (averaged

across climate scenarios, our area burned estimates are between 1.4 and 8.0 times higher than those of Bachelet *et al.* (2005) for the period 2051–2090). Furthermore, our simulations do not dynamically simulate vegetation changes postfire or in response to changes in climate (i.e. vegetation types are static). The greater area burned estimates may be because we used different climate model scenarios to simulate future area burned.

Changes in 21st century carbon storage

Similar to the conclusions of Balshi *et al.* (2007) regarding the dominant drivers responsible for sink activity from 1959 to 2002, we found that both the effects of CO_2 fertilization and climatic variability accounted for the majority of the reported carbon sink across boreal North America for the 21st century for both climate scenarios. In general, the changes in carbon storage simulated in the retrospective simulations of Balshi *et al.* (2007) were more consistent with atmospheric inversion analyses for the set of simulations with CO_2 fertilization. The trajectories of future CO_2 used in this study estimated by the regression approach we employed resulted in 2100 CO_2 concentrations of 1100 and 766 ppmv in the A2 and B2 scenarios, respectively. Other estimates based on the IPCC Third Assessment Report suggest that median values for A2 and B2 scenarios should be around 900 and 700 ppmv, respectively (IPCC 2001). However, climate models that include carbon cycle feedbacks driven by A2 fossil fuel emissions range between 730 and 1020 ppmv atmospheric CO_2 in 2100 depending largely on variability of the terrestrial sink (Friedlingstein *et al.*, 2006). Because our estimates of CO_2 concentration for the A2 and B2 scenarios in 2100 are slightly higher than previously published estimates for these scenarios, the simulations conducted in this study that include the effects of elevated CO_2 concentration should be interpreted as an upper bound of possible CO_2 effects for scenarios that we considered in this study. In our simulations with CO_2 fertilization, the sink activity for the A2 scenario resulted in approximately 24% more carbon stored than the B2 scenario. However, for the simulations that excluded a CO_2 fertilization effect we report a source of carbon from terrestrial ecosystems to the atmosphere. The switch to a source in the simulations that exclude CO_2 fertilization is due to both no carbon sequestration associated with rising CO_2 and lower carbon sequestration in response to climatic variability due to the lack of an interaction effect of CO_2 fertilization with climate (Table 2).

To our knowledge, this study is the first to simulate the effects of empirically derived future fire estimates on the carbon dynamics of the North American boreal

region. The only study that we know of that reports estimates for a portion of our study area is Bachelet *et al.* (2005), which is driven by scenario climates from Canadian and Hadley GCMs. It is important to note that the simulations of Bachelet *et al.* (2005) differ from ours in the trajectories of CO_2 concentration and the inclusion of vegetation dynamics, such as the migration of treeline toward the coast of the Arctic Ocean. Bachelet *et al.* (2005) reported a range of NECB estimates of between 10 and $31 \text{ g Cm}^{-2} \text{ yr}^{-1}$ sequestered by terrestrial vegetation for Alaska for the period 2025–2099. Our estimates of carbon storage over the same period indicate carbon storage of between 18 and $28 \text{ g Cm}^{-2} \text{ yr}^{-1}$ for the simulations that included CO_2 fertilization, which is within the range of Bachelet *et al.* (2005). In contrast, our simulations that exclude CO_2 fertilization estimate a range of between 3.9 and $4.7 \text{ g Cm}^{-2} \text{ yr}^{-1}$ for Alaska, which is below the range of Bachelet *et al.* (2005).

Our simulations for the 21st century also indicate that atmospheric CO_2 fertilization plays a major role in the carbon dynamics of boreal North America. In our simulations, the A2 and B2 scenarios responded differently to the elevated levels of atmospheric CO_2 . Carbon storage increases in response to elevated CO_2 for each decade for the A2 scenario while carbon storage increases and then plateaus for the last three decades of the 21st century for the B2 scenario. This response is likely due to the deceleration of increasing CO_2 concentration.

The increase in carbon storage to warming in our simulations is associated with increases in the availability of soil nitrogen due to warming-enhanced nitrogen mineralization (McGuire *et al.*, 1992; Xiao *et al.*, 1998). The influence of interannual variation in climate on carbon storage simulated by TEM has been documented in previous studies (Tian *et al.*, 1999; McGuire *et al.*, 2001; Euskirchen *et al.*, 2006; Balshi *et al.*, 2007; Clein *et al.*, 2007; Kimball *et al.*, 2007). For the simulations incorporating the effect of atmospheric CO_2 , both climate scenarios indicate that as average decadal temperatures increase, carbon storage associated with climate increases. In contrast, the simulations excluding atmospheric CO_2 fertilization estimate lower sink strength associated with climate.

Our results indicate that it is important to incorporate fire in estimating future carbon dynamics. For the 21st century, we estimate that fire results in a net carbon source to the atmosphere in some regions for simulations that include and exclude atmospheric CO_2 and is larger under the A2 scenario than the B2 scenario. The incorporation of fire activity into our analysis reduces total ecosystem carbon storage through changes in vegetation and soil carbon pools across boreal North

America for the entire 21st century. For the simulations excluding CO₂ fertilization, decades with greater area burned resulted in an overall carbon source to the atmosphere (Figs 7d and 8d) while decades with lower area burned generally resulted in greater carbon sink activity.

Uncertainties and limitations

Several challenges were encountered when coupling future area burned to the current framework of the TEM. The first challenge we encountered was down-scaling future area burned from 2.5 to OS' spatial resolution, which required several assumptions. For the sake of simplicity, we evenly distributed the area burned estimates for each year to every OS cell that occurred within a given 2.5" cell. This area was then distributed to cohorts within each OS' cell based on the number and age of the cohorts in year 2002. Although the accuracy of future stand age distributions and their spatial pattern therefore depends on the accuracy of the stand ages in year 2002, the general shift toward younger forests in response to more frequent fires is a robust result of this study. An added level of uncertainty deals with the assumption that all burnable vegetation types within a given 2.5' cell are available for burning in the future. A third limitation that is not taken into consideration in this study is the potential for grid cells that were not explicitly modeled by Balshi *et al.* (2008) to burn in the future. Changes in climate are likely going to be accompanied by increases in fuel loading in areas that have not burned historically, and therefore more likely to burn if warmer, drier conditions prevail. Accounting for future fire in grid cells that are currently assumed not to burn would likely result in a greater carbon source.

Incorporating the role of dynamic vegetation, temporal changes in fire severity, and other disturbances such as insect outbreaks in future modeling studies is important with respect to capturing a better representation of emissions estimates at the time of fire as well as the carbon dynamics associated with secondary successional processes following fire. One of the main limitations of the current study is that our carbon balance estimates are based on a fixed vegetation distribution that does not change spatially through time. This can be problematic in that regional carbon dynamics can be influenced for several decades following fire due to the differences in the postfire responses of different vegetation types (e.g. deciduous vs. coniferous) (Amiro *et al.*, 2006). This introduces uncertainty with respect to the calculation of NECB and is also important with respect to surface energy feedbacks between terrestrial ecosys-

tems and the climate system (Chapin *et al.*, 2000; McGuire *et al.*, 2006; Randerson *et al.*, 2006).

Under a warming climate, it is also important to recognize the potential of the northward expansion of vegetation types currently absent from particular regions of the boreal forest and the implications this may have on future fire regimes. There is increasing evidence of tree line expansion into tundra (Bachelet *et al.*, 2005; Chapin *et al.*, 2005; Scholze *et al.*, 2006; McGuire *et al.*, 2007) as well as the northward expansion of lodgepole pine (Johnstone & Chapin, 2003) that should be taken into account in future work. Note that there is substantial variability in the rate of northward migration among models that do and do not incorporate demographic and topographic constraints on migration rates (see discussions by MacDonald *et al.*, 1993; Chapin & Starfield, 1997; Rupp *et al.*, 2001; Nielson *et al.*, 2005; Araujo & New, 2006; Araujo & Rahbek, 2006), and some analyses indicate that it will take centuries for substantial migration of northern treeline to occur. Nonetheless, if fire were to migrate into areas currently dominated by other vegetation types (e.g. tundra), the contribution to fire emissions and the overall carbon budget could be significant.

Fire severity influences the amount of total carbon emitted at the time of fire as well as long-term carbon accumulation (Kurz & Apps, 1999; Harden *et al.*, 2000; Balshi *et al.*, 2007). Our implementation of fire severity is static, which does not account for seasonal variations in depth of burn. The importance of accounting for seasonal variation in depth of burn has been addressed in previous studies (Kasischke *et al.*, 2005; Kasischke & Turetsky, 2006) and has great potential to result in different estimates of total carbon emitted than what we report in the current study. Several studies (Wotton & Flannigan, 1993; Flannigan *et al.*, 2000, 2005; Carrailet *et al.*, 2001; Balshi *et al.*, 2008) have shown that a warmer climate results in greater future area burned, which is partially a consequence of longer fire seasons. If fire seasons become longer, there is potential for the alteration of depth of burn (i.e. greater severity) due to the potential for drier conditions in the duff layer in addition to deeper thaw of the soil. Increases in fire severity have the potential to decrease the amount of insulating moss and soil organic layers, which can also feedback to the soil thermal and permafrost regimes through increasing the active layer depth and thawing of permafrost (Hinzman *et al.*, 2003). Interactions between fire severity, soil thermal, and permafrost regimes are therefore important to consider in future work.

With the potential for increases in area burned by wildfire through the 21st century (Fig. 2), the level of fire suppression efforts are also likely to increase. However, the effectiveness of suppression over large areas

and long timescales has been debated (Miyaniishi & Johnson, 2001; Ward *et al.*, 2001) and it is difficult to determine how this may impact large scale carbon dynamics and fire emissions in the future. The issue of fire suppression remains an important issue for predicting future fire regimes (see Balshi *et al.*, 2008) and the effects that those regimes may have on regional carbon dynamics.

Finally, it is important to consider the role of other disturbances (e.g. insects and disease) and how they interact with fire regime across the North American boreal forest. It has been suggested that as climate warms, insect outbreak behavior will intensify (Logan *et al.*, 2003). Because insect outbreaks and disease result in more available fuel for future disturbance by wildfire, there is great potential to alter fire regime due to the potential for larger, more catastrophic fire events. Incorporating the response of disease and insect disturbances to future climate change and the interactions between these disturbances and fire regime will be essential to improve current carbon balance estimates of the future.

Acknowledgements

Funding for this study was provided by grants from the National Science Foundation Biocomplexity Program (ATM-0120468) and Office of Polar Programs (OPP-0531 047, OPP-0328282, and OPP 0327664); the National Aeronautics and Space Administration North America Carbon Program (NNG05GD25G); and the Bonanza Creek LTER (Long-Term Ecological Research) Program (funded jointly by NSF grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JVf1261952-231). This study was also supported in part by a grant of HPC resources from the Arctic Region Supercomputing Center at the University of Alaska Fairbanks as part of the Department of Defense High Performance Computing Modernization Program.

References

- Allen AS, Andrews JA, Finzi AC, Matamala R, Richter DO, Schlesinger WH (2000) Effects of free-air CO₂ enrichment (FACE) on belowground processes in a *Pinus taeda* forest. *Ecological Applications*, 10, 437–448.
- Amiro BD, Chen JM, Liu J (2000) Net primary productivity following forest fire for Canadian ecoregions. *Canadian Journal of Forest Research*, 30, 939–947.
- Amiro BD, Orchansky AL, Barr AG *et al.* (2006) The effect of post-fire stand age on the boreal forest energy balance. *Agricultural and Forest Meteorology*, 140, 41–50.
- Araujo MB, New M (2006) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, 22, 42–47.
- Araujo MB, Rahbek C (2006) How does climate change affect biodiversity? *Science*, 313, 1396–1397.
- Bachelor O, Lenihan J, Neilson R, Drapek R, Kittel T (2005) Simulating the response of natural ecosystems and their fire regimes to climatic variability in Alaska. *Canadian Journal of Forest Research*, 35, 2244–2257.
- Balshi MS, McGuire AD, Duffy PO *et al.* (2008) Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology*, 15, 578–600.
- Balshi MS, McGuire AD, Zhuang Q *et al.* (2007) The role of historical fire disturbance in the carbon dynamics of the pan-boreal region: a process-based analysis. *Journal of Geophysical Research*, 112, G02029, doi: 10.1029/2006JG000380.
- Calef MP, McGuire AD, Chapin FS III (2008) Human influences on wildfire in Alaska from 1988 through 2005: an analysis of the spatial patterns of human impacts. *Earth Interactions*, 12, 1–17.
- Canadell JG, Pataki DE, Gifford R *et al.* (2007) Saturation of the terrestrial carbon sink. In: *Terrestrial Ecosystems in a Changing World. The 1GBP Series* (eds Canadell JG, Pataki D, Pitelka U, pp. 59–73. Springer-Verlag, Berlin.
- Carcaillet C, Bergeron Y, Richard PJH, Frechette B, Gauthier S, Prairie YT (2001) Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology*, 89, 930–946.
- Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science*, 290, 1148–1151.
- Chambers SO, Chapin FS III (2003) Fire effects on surface-atmosphere exchange in Alaskan black spruce ecosystems: implications for feedbacks to regional climate. *Journal of Geophysical Research*, 108(01), doi: 10.1029/2001JD000530.
- Chapin FS III, McGuire AD, Randerson J *et al.* (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, 6 (Suppl. 1), 211–223.
- Chapin FS III, Starfield AM (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change*, 35, 449–461.
- Chapin FS III, Sturm M, Serreze MC *et al.* (2005) Role of land-surface changes in arctic summer warming. *Science*, 310, 657–660.
- Chapin FS III, Woodwell GM, Randerson J *et al.* (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, 9, 1041–1050.
- Chen J, Chen W, Liu J *et al.* (2000) Annual carbon balance of Canada's forests during 1895–1996. *Global Biogeochemical Cycles*, 14, 839–849.
- Chen JM, Chen B, Higuchi K *et al.* (2003) Spatial distribution of carbon sources and sinks in Canada's forests. *Tellus, Series B*, 55, 622–641.
- Clein JS, Kwiatkowski B, McGuire AD *et al.* (2000) Modeling carbon responses of tundra ecosystems to historical and projected climate: a comparison of a plot- and a global-scale ecosystem model to identify process-based uncertainties. *Global Change Biology*, 6, S127–S140.
- Clein JS, McGuire AD, Euskirchen ES, Calef MP (2007) The effects of different climate input data sets on simulated carbon dynamics in the Western Arctic. *Earth Interactions*, 11, doi: 10.1175/EI229.1.

- Clein JS, McGuire AD, Zhang X *et al.* (2002) Historical and projected carbon balances of mature black spruce ecosystems across North America: the role of carbon-nitrogen interactions. *Plant and Soil*, 242, 15–32.
- DeLucia EH, Hamilton JG, Naidu SL *et al.* (1999) Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science*, 284, 1177–1179.
- Euskirchen ES, McGuire AD, Chapin FS III (2007) Energy feedbacks to the climate system associated with snow cover dynamics in northern high latitudes during warming periods of the 20th Century. *Global Change Biology*, 13, 2425–2438.
- Euskirchen SE, McGuire AD, Kicklighter DW *et al.* (2006) Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology*, 12, 731–750.
- Flannigan MD, Bergeron Y, Engelmark O, Wotton BM (1998) Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science*, 9, 469–476.
- Flannigan MD, Logan KA, Amiro BD, Skinner WR, Stocks BJ (2005) Future area burned in Canada. *Climate Change*, 72, 1–16.
- Flannigan MD, Stocks BJ, Wotton BM (2000) Climate change and forest fires. *The Science of the Total Environment* 262, 221–229.
- Flato GM, Boer GJ (2001) Warming asymmetry in climate change simulations. *Geophysical Research Letters*, 28, 195–198.
- French NHF, Kasischke ES, Stocks BJ, Mudd JP, Martell DL, Lee BS (2000) Carbon release from fires in the North American boreal forest. In: *Fire, Climate Change and Carbon Cycling in the Boreal Forest*, Ecological Studies Vol. 138 (eds Kasischke ES, Stocks BJ), pp. 377–388. Springer-Verlag, New York.
- Friedlingstein P, Cox P, Betts R *et al.* (2006) Climate-carbon cycle feedback analysis: results from the C⁴MIP Model Comparison. *Journal of Climate*, 19, 3337–3353.
- Gillett NP, Weaver AJ, Zwiers FW, Flannigan MD (2004) Detecting the effect of climate change on Canadian forest fires. *Geophysical Research Letters*, 31, L8211, doi: 10.1029/2004GL020876.
- Global Soil Data Task Group (2000) *Global Gridded Surfaces of Selected Soil Characteristics (International Geosphere-Biosphere Programme - Data and Information System)*, Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee.
- Harden JW, Neff JC, Sandberg DV *et al.* (2004) Chemistry of burning the forest floor during the FROSTFIRE experimental burn, interior Alaska, 1999. *Global Biogeochemical Cycles*, 18, GB3014, doi: 10.1029/2003GB002194.
- Harden JW, Trumbore SE, Stocks BJ *et al.* (2000) The role of fire in the boreal carbon budget. *Global Change Biology*, 6 (Suppl. 1), 174–184.
- Hicke JA, Asner GT, Kasischke ES *et al.* (2003) Postfire response of North American boreal forest net primary productivity analyzed with satellite observations. *Global Change Biology*, 9, 1145–1157.
- Hinzman LD, Fukuda M, Sandberg DY, Chapin FS III, Dash D (2003) FROSTFIRE: an experimental approach to predicting the climate feedbacks from a changing boreal fire regime. *Journal of Geophysical Research*, 108, 8153, doi: 10.1029/2001J D00415.
- Hungate B, Dukes JS, Shaw MR, Luo Y, Field CB (2003) Nitrogen and climate. *Science*, 302, 1512–1513.
- IPCC (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to The Third Assessment Report of the intergovernmental Panel on Climate Change* (eds Houghton JT, Ding Y, Griggs D) *et al.*, Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.
- Johnstone JF, Chapin FS III (2003) Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology*, 9, 1401–140Y.
- Joos F, Prentice IC, House J (2002) Growth enhancement to global atmospheric change as predicted by terrestrial ecosystem models: consistent with US forest inventory data. *Global Change Biology*, 8, 299–303.
- Kalnay E, Kanamitsu M, Kistler R *et al.* (1996) The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, 77, 437–470.
- Kasischke E, Christensen NL Jr, Stocks BJ (1995) Fire, global warming, and the carbon balance of boreal forests. *Ecological Applications* 5, 437–451.
- Kasischke ES, Hyer EJ, Novelli PC *et al.* (2005) Influences of boreal fire emissions on Northern Hemisphere atmospheric carbon and carbon monoxide. *Global Biogeochemical Cycles*, 19, GB1012, doi: 10.1029/2004GB002300.
- Kasischke ES, Rupp TS, Verbyla DL (2006) Fire trends in the Alaskan boreal forest. In: *Alaska's Changing Boreal Forest* (eds Chapin FS III, Oswood MW, Van Cleve K, Viereck LA, Verbyla DL), pp. 285–301. Oxford University Press, New York, USA.
- Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region - spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters*, 33, L09703, doi: 10.1029/2006GL025677.
- Kasischke ES, Williams D, Barry D (2002) Analysis of the patterns of large fires in the boreal forest region of Alaska. *International Journal of Wildland Fire*, 11, 131–144.
- Keeling CD, Whorf TP (2005) Atmospheric CO₂ records from sites in the SIO air sampling network. In: *Trends: A Compendium of Data on Global Change*. Carbon dioxide information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, TN, USA.
- Kimball JS, Zhao M, McGuire AD *et al.* (2007) Recent climate driven increases in vegetation productivity for the western Arctic: evidence of an acceleration of the northern terrestrial carbon cycle. *Earth: interactions*, 11, doi: 10.1175/E1180.1.
- Korner C, Asshoff R, Bignucolo O *et al.* (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. *Science*, 309, 1360–1362.
- Kurz WA, Apps M (1999) A 70-year retrospective analysis, of carbon fluxes in the Canadian forest sector. *Ecological Applications*, 9, 526–547.
- Logan JA, Regniere J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and Environment*, 1, 130–137.
- Long SP, Ainsworth EA, Leakey ADB, Nosberger J, Ort DR, (2006) Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science*, 312, 1918–1921.

- Lovelock CE, Winter K, Mersits R, Popp M (1998) Responses of tropical tree species to elevated CO₂ in a forest clearing. *Oecologia*, 116, 207-218.
- Luol Y, Field CB, Jackson RB (2006) Does nitrogen constrain carbon cycling, or does carbon input stimulate nitrogen cycling? *Ecology*, 87, 3-4.
- Luo YQ, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, 54, 731-739.
- MacDonald GM, Edwards TWD, Moser KA, Pienitz R, Smol JP (1993) Rapid response of tree line vegetation and lakes to past climate warming. *Nature*, 361, 243-246.
- McGuire AD, Apps M, Chapin FS (2004) Land cover disturbances and feedbacks to the climate system in Canada and Alaska. In: *Land Change: Science: Observing, Monitoring and Understanding Trajectories of Change on the Earth's Surface* (eds Gutman G *et al.*), pp. 139-161. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- McGuire AD, Chapin FS III, Walsh JE, Wirth C (2006) Integrated regional changes in arctic climate feedbacks: implications for the global climate system. *Annual Review of Environment and Resources* 31,61-91.
- McGuire AD, Chapin FS III, Wirth C *et al.* (2007) Responses of high latitude ecosystems to global change: potential consequences for the climate system. In: *Terrestrial Ecosystems in a Changing World* (eds Canadell JG, Pataki DE, Pitelka LF), pp. 297-310. The IGSP Series, Springer-Verlag, Berlin.
- McQuinn AD, Clein J, Melillo JM (2000a) Modeling carbon responses of tundra ecosystems to historical and projected climate: the sensitivity of pan-arctic carbon storage to temporal and spatial variation in climate. *Global Change Biology*, 6, S141-S159.
- McGuire AD, Melillo JM, Joyce LA (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles*, 6, 101-124.
- McGuire AD, Melillo JM, Kicklighter DW (1997) Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles*, 11,173-189.
- McGuire AD, Melillo JM, Randerson JT (2000b) 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 AD, Sitch S, Cee Jin JS (2001) Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO₂, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles*, 15, 183-206.
- McGuire AD, Walsh J, Kimball J *et al.* (2008) The Western Arctic Linkage Experiment (WALE): overview and synthesis. *Earth Interactions*, 12, doi: 10.1175/2008E1239.1.
- McGuire AD, Wirth C, Apps M *et al.* (2002) Environmental variation, vegetation distribution, carbon dynamics and water/energy exchange at high latitudes. *Journal of Vegetation Science*, 13,301-314.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature*, 63, 234-240.
- Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, 25, 693-712.
- Miyaniishi K, Johnson EA (2001) Comment - A reexamination of the effects of fire suppression in the boreal forest. *Canadian Journal of Forest Research*, 31,1462-1466.
- Murphy PI, Mudd JP, Stocks BJ *et al.* (2000) Historical fire records in the North American boreal forest. In: *Fire, Climate Change, and Carbon Cycling in the Boreal Forest, Ecological Studies*, Vol. 138 (eds Kasischke ES, Stocks BJ), pp. 274-288. Springer-Verlag, New York.
- Nakicenovic N, Swart R. (eds) (2000) *Intergovernmental Panel on Climate Change, Special Report on Emissions Scenarios*: Cambridge University Press, Cambridge, UK.
- National Geophysical Data Center (NGDC) (1994) *TerrainBase v. 1.1, 5-minute Digital Terrain Model Data*. Boulder, Colorado.
- Nielson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thompson K (2005) Forecasting regional to global plant migration in response to climate change. *Bioscience*, 55, 749-759.
- Norby RJ, Gunderson CA, Wullschlegel SD, O'Neill EG, McCracken MK (1992) Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. *Nature*, 357, 322-324.
- Oren R, Ellsworth DS, Johnsen KH (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature*, 411, 469-472.
- Pan Y, Melillo JM, McGuire AD *et al.* (1998) Modeled responses of terrestrial ecosystems to elevated atmospheric CO₂: a comparison of simulation studies among the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia*, 114, 389-404.
- Peng C, Apps MJ (1999) Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecological Modelling*, 122, 175-193.
- Raich JW, Rastetter EB, Melillo JM *et al.* (1991) Potential net primary productivity in South America: application of a global model. *Ecological Application*, 1, 399-429.
- Randerson JT, Liu L, Plattner MG *et al.* (2006) The impact of boreal forest fire on climate warming. *Science*, 314, 1130-1132.
- Reich PB, Hungate B, Luo Y (2006) Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution and Systematics*, 37,611-636.
- Rupp TS, Chapin FS III, Starfield AM (2001) Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. *Climatic Change*, 48,399-416.
- Rupp TS, Chen X, Olson M, McGuire AD (2007) Sensitivity of simulated boreal fire dynamics to uncertainties in climate drivers. *Earth Interactions*, 11, doi: 10.1175/E1189.1.
- Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature*, 411, 466-469.

- Scholze M, Knorr W, Arnell NW, Prentice IC (2006) A climate-change risk analysis for world ecosystems. *Proceedings of the National Academy of Science*, 103, 13116-13120.
- Sokolov AP, Kicklighter DW, Melillo JM *et al.* (2008) Consequences of considering carbon/nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. *Journal of Climate*, 21, 3776-3796.
- Stocks B, Fosberg MA, Lynham T *et al.* (1998) Climate change and forest fire potential in Russian and Canadian boreal forests. *Climatic Change*, 38, 1-13.
- Stocks BJ, Mason JA, Todd JB *et al.* (2002) Large forest fires in Canada, 1959-1997. *Journal of Geophysical Research*, 108, 01, doi: 10.1029/2001J0000484.
- Thonicke K, Venevsky S, Sitch S *et al.* (2001) The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. *Global Ecology and Biogeography*, 10, 661-677.
- Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich J (1999) The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO₂ in the United States. *tellus*, 51B, 414-452.
- Venevsky S, Thonicke K, Sitch S, Cramer W (2002) Simulating fire regimes in human-dominated ecosystems: Iberian Peninsula case study. *Global Change Biology*, 8, 984-998.
- Ward PC, Tithcott AG, Wotton BM (2001) Reply - a re-examination of the effects of fire suppression in the boreal forest, *Can. Journal of Forensic Research*, 31, 1467-1480.
- Wirth C, Schulze ED, Luhker B *et al.* (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant and Soil*, 242, 41-63.
- Wotton BM, Flannigan MD (1993) Length of the fire season in a changing climate. *Forestry Chronicle*, 69, 187-192.
- Xiao X, Melillo JM, Kicklighter DW *et al.* (1998) Transient climate change and net ecosystem production of the terrestrial biosphere. *Global Biogeochemical Cycles*, 12, 345-360.
- Zhuang Q, McGuire AD, Harden J, O'Neill KP, Romanovsky VE, Yarie J (2002) Modeling soil thermal and carbon dynamics of a fire chronosequence in interior Alaska. *Journal of Geophysical Research*, 107, 8147, doi: 10.1029/2001JD001244.
- Zhuang Q, McGuire AD, Melillo JM (2003) Carbon cycling in extratropical terrestrial ecosystems of the Northern Hemisphere during the 20th Century: a modeling analysis of the influences of soil thermal dynamics. *Tellus*, 55B, 751-776.
- Zhuang Q, Melillo JM, Felzer BS (2006) CO₂ and CH₄ exchanges between land ecosystems and the atmosphere in northern high latitudes over the 21st century. *Geophysical Research, letter*, 33, L17403, doi: 10.1029/2006GL026972.
- Zhuang Q, Romanovsky VE, McGuire AD (2001) Incorporation of a permafrost model into a large-scale ecosystem model: evaluation of temporal and spatial scaling issues in simulating soil thermal dynamics. *Journal Geophysical Research*, 106, 33649-33670.