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Enhanced terrestrial carbon uptake in the Northern High Latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections

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Abstract

The ongoing and projected warming in the northern high latitudes (NHL; poleward of 60° N) may lead to dramatic changes in the terrestrial carbon cycle. On the one hand, warming and increasing atmospheric CO₂ concentration stimulate vegetation productivity, taking up CO₂. On the other hand, warming accelerates the decomposition of soil organic matter (SOM), releasing carbon into the atmosphere. Here, the NHL terrestrial carbon storage is investigated based on 10 models from the Coupled Carbon Cycle Climate Model Intercomparison Project. Our analysis suggests that the NHL will be a carbon sink of 0.3 ± 0.3 Pg C yr⁻¹ by 2100. The cumulative land organic carbon storage is modeled to increase by 38 ± 20 Pg C over 1901 levels, of which 17 ± 8 Pg C comes from vegetation (43%) and 21 ± 16 Pg C from the soil (8%). Both CO₂ fertilization and warming enhance vegetation growth in the NHL. Although the intense warming there enhances SOM decomposition, soil organic carbon (SOC) storage continues to increase in the 21st century. This is because higher vegetation productivity leads to more turnover (litterfall) into the soil, a process that has received relatively little attention. However, the projected growth rate of SOC begins to level off after 2060 when SOM decomposition accelerates at high temperature and then catches up with the increasing input from vegetation turnover. Such competing mechanisms may lead to a switch of the NHL SOC pool from a sink to a source after 2100 under more intense warming, but large uncertainty exists due to our incomplete understanding of processes such as the strength of the CO_2 fertilization effect, permafrost, and the role of soil moisture. Unlike the CO₂ fertilization effect that enhances vegetation productivity across the world, global warming increases the productivity at high latitudes but tends to reduce it in the tropics and mid-latitudes. These effects are further enhanced as a result of positive carbon cycle-climate feedbacks due to additional CO₂ and warming.

Keywords: biomass turnover, C4MIP, carbon-climate feedback, climate change, CO₂, Northern High Latitudes, NPP, SOM decomposition, terrestrial carbon

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Introduction

The carbon cycle is an important biogeochemical cycle in the climate system because carbon dioxide (CO₂) is a principal greenhouse gas that contributes significantly to

Correspondence: Ning Zeng, Department of Atmospheric and Oceanic Science, University of Maryland, College Park, MD 20742-2425, USA, tel. +1 301 4055377, fax +1 301 3149482, e-mail: zeng@atmos.umd.edu global warming (IPCC, 2007). The amount of CO_2 in the atmosphere is not only dependent on anthropogenic fossil fuel emission, but also on the exchange of carbon fluxes between the atmosphere, land, and ocean. The carbon exchanges between the atmosphere and ecosystems are in turn highly affected by climate change. Therefore, understanding the interaction between climate and carbon cycle is essential for the accurate projection of the evolution of the biogeochemical cycles and climate.

During the past decades, the northern high latitudes (NHL: poleward of 60°N) have witnessed dramatic changes, with annual average temperatures increasing by 1–2 °C in northern Eurasia and northwestern North America (Arctic Climate Impact Assessment, 2005). This warming is much larger than the increase of global average surface temperature of 0.7 °C over the 20th century (IPCC, 2007). Snow/ice-albedo feedback, dynamical feedbacks associated with the poleward heat transport of the oceans and atmosphere (Holland & Bitz, 2003; Alexeev *et al.*, 2005; Kaplan & New, 2006), and internal feedbacks associated with polar processes (Overland *et al.*, 2004) have been traditionally attributed as the cause of this warming.

This significant increase in temperature affects two centrally important NHL biomes: boreal forest and tundra (Fig. 1). Satellite and phenology studies suggest that during the past several decades the boreal forests have experienced greening and an increase in photosynthetic activity. (Keeling *et al.*, 1996; Myneni *et al.*, 1997; Tucker *et al.*, 2001; Zhou *et al.*, 2001; Lucht *et al.*, 2002; Devi *et al.*, 2008). Such a greening can be associated with a 10–20-day lengthening of the growing season (Tucker *et al.*, 2001; Zhou *et al.*, 2001; Thompson *et al.*, 2004; Euskirchen *et al.* 2006; Linderholm, 2006; Schwartz *et al.*, 2006; Piao *et al.*, 2008). Treeline advance in the boreal forests (Lloyd *et al.*, 2003) and

increasing shrubiness of the tundra (Myneni *et al.*, 1997; Sturm *et al.*, 2001) also contribute to the greening. The increase in photosynthetic activity may lead to longterm increases in vegetation carbon storage and changes in vegetation cover, which in turn affects the climate system. However, it is important to note that the greening has not been necessarily uniform, as some areas have decreased in productivity (Sirois & Payette, 1991; Arseneault & Payette, 1992; Goetz *et al.*, 2005).

On the other hand, frozen soils are prevalent in the tundra and large parts of the boreal forest, with a northsouth gradient from continuous-to-discontinuous permafrost (Brown & Romanovsky, 2008). With low ambient temperatures, waterlogged soils and slow drainage, the permafrost-affected ecosystems have been slowly accumulating a large amount of organic carbon (Zimov et al., 2006; Sitch et al., 2007). The terrestrial ecosystems lose carbon primarily through respiration (autotrophic and heterotrophic). When the frozen soil begins to melt in response to rising temperatures, the metabolism of soil microbes is enhanced and the decomposition of soil organic matter (SOM) is accelerated. This leads to an increase of soil organic carbon (SOC) release to the atmosphere (Khvorostyanov et al., 2008). One estimate suggests that global warming could thaw 25% of the permafrost by 2100, thus rendering about 100 Pg C SOC vulnerable to decay (Davidson et al., 2006). To date,



Fig. 1 Boreal vegetation distribution in the northern high latitudes (NHL) modified from Montaigne (2002). The area poleward of 60°N (circled in black) is defined as the NHL.

however, such processes involving SOC exchanges are poorly understood and the amount of potential carbon release is highly uncertain (Melillo *et al.*, 2002; Bond-Lamberty *et al.*, 2004; Eliasson *et al.*, 2005; Lawrence & Slater, 2005; Bronson *et al.*, 2008).

The carbon uptake by vegetation and the carbon release from the soil due to future warming will therefore determine whether the NHL becomes a source or sink of carbon in the future. Many studies have used offline simulations of vegetation-carbon models forced by the IPCC climate projections to investigate the future effects of CO₂ fertilization, climate change, land-use change, and nutrient limitation on NHL ecosystems (McGuire et al., 2000; Cramer et al., 2001; Callaghan et al., 2004, 2005; Schaphoff et al., 2006; Sitch et al., 2007). Several of these studies suggest that both a greening of vegetation and a loss of SOC will occur. Depending on which factor dominates, the NHL can either be a sink or a source of carbon in the future. However, few studies have considered carbon cycle-climate coupling in the NHL (McGuire et al., 2006). Although off-line simulations project the response of the ecosystem to changes in the physical climate, feedback from the ecosystem to the climate system is generally not considered. Fully coupled models allow for a two-way interaction between vegetation and climate, making them potentially more realistic in studying the long-term response to climate. Recently, fully coupled three-dimensional carbon cycle-climate models have been used to study the interaction between the global carbon cycle and climate (Cox et al., 2000; Friedlingstein et al., 2001; Joos et al., 2001; Zeng et al., 2004; IPCC, 2007; Matthews et al., 2007). Most of these studies show a positive feedback to the climate system. That is, under a warmer scenario, ecosystems will further reduce their capacity to absorb anthropogenic emissions, leading to more CO₂ being retained in the atmosphere and an acceleration of global warming. However, quantifying and predicting this carbon cycle-climate feedback is difficult because of limited understanding of the processes by which carbon and associated nutrients are transformed and/or recycled within ecosystems (Heimann & Reichstein, 2008). Large uncertainties from various model parameterizations and modeling protocols have highlighted an urgent need for model intercomparsion to better ascertain the interaction between climate and the carbon cycle.

In the Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP), 11 climate modeling groups have used their fully coupled carbon cycle– climate models to investigate such interactions, with particular emphasis on the feedback processes involved (Friedlingstein *et al.*, 2006). The modeling protocol includes: (1) The anthropogenic emission of CO₂ from the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A2 scenario was used as the same external forcing for each fully coupled carbon cycle-climate model; (2) Two separate simulations were run: a fully coupled interactive carbon cycle-climate case and an uncoupled case, wherein a prescribed climate was used (radiative CO₂ concentration was kept at preindustrial levels), with the vegetation and carbon components seeing the effect of increasing CO₂ concentration on photosynthesis. Carbon cycle-climate feedback was then calculated as the difference between the two simulations. Friedlingstein et al. (2006) found a positive carbon cycle-climate feedback from all C4MIP models in the 21st century, on the global scale. Owing to this positive feedback, there is an additional 20–200 ppm CO₂ in the atmosphere by 2100, leading to a 0.1-1.5 °C warming across the C4MIP models. The majority of the models show a reduction of the terrestrial carbon uptake in the tropics due to such a climate feedback (Fig. 1 in Friedlingstein et al., 2006).

Climate change during the past decades has been transforming the physical, biological, and societal conditions in the NHL (Arctic Climate Impact Assessment, 2005). In this study, we investigate the evolution of the NHL terrestrial organic carbon storage under climate change using a suite of fully coupled carbon cycleclimate C4MIP models. Our analysis is unique due to the large number of terrestrial carbon models and the inclusion of carbon–climate feedback. The key scientific questions we address are:

- Will the NHL terrestrial biosphere become a carbon sink or a source in the future?
- What will be the relative roles of vegetation vs. soil? What are the mechanisms? Specifically, what are the effects of CO₂ fertilization and climate change (mainly intense warming in the NHL) on photosynthesis and SOM decomposition?
- Are future projections of terrestrial carbon change by fully coupled carbon cycle–climate models consistent with the current observed greening and the northward shift of vegetation distributions over the past decades?

Models, data, and methodology

The principal focus of our study is to investigate the terrestrial organic carbon storage change in the high latitude regions poleward of 60°N (region poleward of the dark brown circle in Fig. 1) in coupled carbon cycleclimate systems. The data used in this study are based on the multimodel simulations provided by C4MIP

(http://c4mip.lsce.ipsl.fr/), which is a joint project between the International Geosphere-Biosphere Program (IGBP) and the World Climate Research Program (WCRP). The terrestrial carbon models used in the 11 coupled carbon-climate models can be found in Table 1, and the reader is referred to Friedlingstein *et al.* (2006) for a detailed description of the models. We excluded the LLNL model because it is affected by a large drift in the NHL during the 20th century due to imperfect model spin-up (Bala et al., 2006). Our analysis thus includes only 10 models, of which HadCM3LC and UVic use the same land carbon component [Met Office Surface Exchange Scheme (MOSES)/Top-Down Representation of Interactive Foliage and Flora including Dynamics (TRIFFID)], and CLIMBER2-LJP and BERN-CC similarly share the common Lund-Potsdam-Jena (LPJ) vegetation model component. All the C4MIP groups used the same anthropogenic fossil fuel emissions from Marland et al. (2005) from the beginning of the industrial period until 2000 and the IPCC SRES A2 scenario for the 2000-2100 period. The SRES A2 scenario is among the highest emissions scenarios provided by the IPCC. The coupled simulations in the C4MIP have climate and carbon components that interact freely, thus representing the complete carbon cycle-climate coupling. The uncoupled simulation case treats CO₂ as a nonradiatively active gas (so the carbon cycle experiences no CO₂-induced climate change), while the ecosystems still see increasing CO₂ concentration. The difference between coupled and uncoupled simulations is therefore a measure of the effects due to carbon cycleclimate feedback (Friedlingstein et al., 2006).

Each modeling group provided a standard output time-series of total fossil fuel emissions, simulated global atmospheric CO_2 concentration, surface temperature, terrestrial Net Ecosystem Production (NEP), ocean net CO_2 flux, net primary production (NPP), Heterotrophic Respiration (R_h), and vegetation carbon and

SOC pools for both global and band-averaged regions: 90–30°S, 30–0°S, 0–30°N, 30–60°N, 60–90°N. This study focuses on the terrestrial regions poleward of 60°N, which includes a part of the boreal forest and the whole tundra region. Although the period of the C4MIP simulations begins from 1860 for most models, we have chosen the common period of 1901–2100 for our analysis. Globally averaged quantities are used only as a reference for the NHL comparisons. The results are presented as the individual response of the 10 models, and/or as the mean of the C4MIP models.

Analysis and results

NHL terrestrial carbon storage change in the 21st century

The NHL terrestrial ecosystems store a large amount of carbon in boreal forests and frozen soil (Zimov et al., 2006; Sitch et al., 2007). Before analyzing the projected 21st century change of the NHL terrestrial carbon storage in the C4MIP models, we examined the NHL vegetation carbon and SOC from 1901 to 1910 in the individual models (Fig. 2b), and compared this with the global totals (Fig. 2a). Globally, the C4MIP models simulate a mean total land organic carbon amount of 2046 Pg C with a 95% confidence interval (based on Student's t-test) of 1637-2456 Pg C. The vegetation carbon pool contains 279-937 PgC and the soil contains 999–2152 Pg C. The C4MIP model-mean indicates that the storage of SOC is about 2.5 times that of vegetation, signifying that soil is a major carbon reservoir for land organic carbon on the global scale (Post et al., 1982). While the C4MIP models have similar global land organic carbon pool sizes, there is a wide range in the amount of carbon stored in the NHL in the simulations (Fig. 2b). For example, the mean of the models indicates that the NHL contains about 15% of the total global organic terrestrial carbon. IPSL-CM4-LOOP has 65 Pg C

 Table 1
 The terrestrial carbon models used by each individual member of the C4MIP group

C4MIP models	Terrestrial carbon models	Dynamic vegetation model?	Temporal coverage
BERN-CC	LPJ	Yes	1765–2100
CLIMBER2-LPJ	LPJ	Yes	1901-2100
CCSM-1	LSM, CASA	No	1820-2100
HadCM3LC	TRIFFID	Yes	1860-2100
IPSL-CM2C	SLAVE	No	1860-2099
IPSL-CM4-LOOP	ORCHIDEE	No	1860-2099
MPI	JSBACH	No	1860-2099
FRCGC	Sim-CYCLE	No	1850-2099
UVic	TRIFFID	Yes	1860-2100
UMD	VEGAS	Yes	1860–2100

For more details of the atmospheric and oceanic components, refer to Table 1 in Friedlingstein *et al.* (2006). C4MIP, Coupled Carbon Cycle Climate Model Intercomparison Project.



Fig. 2 Carbon storage in the vegetation and soil modeled by the 10 Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) models and the inter model mean for: (a) Global; (b) northern high latitudes (NHL). The stored carbon is calculated based on 1901–1910 for all models. Soil organic carbon (SOC) is indicated in black, and vegetation in gray. Most of the carbon is locked in the soil particularly in the NHL. Units of storage are in PgC.

stored in the NHL land ecosystem, which is only about 4% of its total global, while CLIMBER-LPJ contains 568 Pg C in the NHL, about 21% of its total global, and UMD has the largest percentage, at 30%. The NHL vegetation stores only 6% of the total global vegetation carbon, as compared with 15% of the model-mean total land organic carbon. The model-mean SOC stored in the NHL is about seven times that of the vegetation carbon in the NHL. This is because the low ambient temperature causes most of the carbon to be stored in the NHL soil (Post *et al.*, 1982; Chapin & Matthews, 1993; McGuire & Hobbie, 1997).

In the past two decades, winter in the northern high latitudes has experienced some of the most rapid changes on Earth, warming almost 2.5 times as fast as the globe (Liu *et al.*, 2007). The atmosphere–ocean coupled general circulation models (AOGCMs) project

that the global near-surface atmosphere will warm by 2°C relative to preindustrial temperatures between 2026 and 2060, at which stage the mean annual temperature over the Arctic region (60-90°N) will have increased by 3.2-6.6 °C (Kaplan & New, 2006). Consistent with these results, the model-mean of the C4MIP members projects that by 2100, the surface temperature in the NHL will increase by 5.6 °C, in contrast to an increase of 3.2 °C for the global average (Fig. 3). Most models show an intense warming in the NHL, at nearly double the rate of the global warming projection through 2100, except for UMD, which does not have interactive snow or sea ice. MPI, FRCGC, and IPSL-CM4-LOOP even project a 7–8 °C warming in the NHL. The C4MIP model-mean warming in the NHL during 1901-2000 is 0.8 °C with a 95% confidence interval of 0.48–1.13 °C. This value is comparable to the observed



Fig. 3 Temperature increase from 1901 to 2100 projected by the fully coupled simulations from Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) models for global mean (gray diamond) and northern high latitudes (NHL) (black circle).

0.82 °C/century warming trend, calculated using surface air temperature data from the NASA Goddard Institute for Space Studies (GISS) (Hansen *et al.*, 1999) (figure not shown).

In the late 2100s the NHL is simulated to be a carbon sink of 0.3 Pg C yr^{-1} from the model-mean of C4MIP (Fig. 4c). With the exception of FRCGC, the other nine models all project that the NHL ecosystem will take up carbon from the atmosphere throughout the 21st century (positive NEP; Fig. 4a). The NEP from the models ranges from 0.1 to 1.0 Pg C yr^{-1} . The intermodel differences generally increase with time (Fig. 4c). However, the model-mean NEP carbon uptake shows a tendency of leveling off or even decreasing around 2060. This leveling-off is particularly visible in the HadCM3LC, FRCGC, and BERN-CC models. The time integral of NEP is the amount of carbon the land takes up. The mean uptake of terrestrial carbon by 2100 is 38 Pg C with a range of 17–82 Pg C in the C4MIP models (Fig. 4b and d). Because the models differ significantly in their degree of warming at a given time (Fig. 3), we also analyzed the NEP change as a function of temperature, and found a typical value of 0.2 Pg C yr^{-1} for a 3° warming that tends to level off with strong warming.

The changes in the vegetation carbon and the SOC are shown in Fig. 5a and b. The mean of the C4MIP models shows that the NHL vegetation carbon storage increases from 40 Pg C in 1901 to 57 Pg C by 2100 (17 Pg C, or 43%). The SOC increases from 262 to 283 Pg C (21 Pg C, or 8%). Although the SOC increase is larger than vegetation increase, but the percentage change is much smaller. This SOC pool is currently protected from release to the atmosphere by cold and waterlogged conditions in the NHL and is considered to be highly

susceptible to changes in temperature and permafrost thawing in the 21st century. In contrast to the estimates of Davidson *et al.* (2006), the C4MIP results suggest that at least in the 21st century, the soil in the NHL may not lose carbon to the atmosphere. This is not necessarily inconsistent with Davidson *et al.* (2006) who considered potential loss of permafrost carbon. But this apparent 'suppression' of warming-induced increase in SOM decomposition in the C4MIP models still comes as somewhat of a surprise.

To better understand this, the carbon budgets of the vegetation and soil were examined separately. Although it is common to use NPP as an indicator of the vegetation productivity and R_h for SOC change, these variables do not directly measure the changes of vegetation carbon and SOC storage. Examination of the mechanisms controlling the vegetation carbon and the SOC exchange processes also involves the following variables: (1) vegetation turnover into soil (T_{ov}), i.e. litterfall, (2) growth rate of vegetation carbon (d C_{vege}/dt), (3) growth rate of SOC (d C_{soil}/dt). Together with NPP and R_h , these five variables are related as

$$\frac{\mathrm{d}C_{\mathrm{vege}}}{\mathrm{d}t} = NPP - T_{\mathrm{ov}},\tag{1}$$

$$\frac{\mathrm{d}C_{\mathrm{soil}}}{\mathrm{d}t} = T_{\mathrm{ov}} - R_{\mathrm{h}}.$$
(2)

Research in global carbon cycle modeling has paid relatively little attention to vegetation turnover T_{ov} . However, as seen clearly in the above two equations, this is the source and driver of SOC, and thus is an important bridge linking the vegetation carbon and



Fig. 4 Changes of net ecosystem production (NEP) and total land organic carbon in the northern high latitudes (NHL) during 1901–2100 in Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) coupled simulations. (a) and (c) NEP; (b) and (d) Total land organic carbon change. Colored lines in (a) and (b) are for individual C4MIP models; (c) and (d) show the multimodel mean (black solid line) and the $\pm 1\sigma$ spread (gray shading). The change in total land organic carbon is relative to 1901. A 6-year running mean is applied to all the curves. Units are PgC yr⁻¹ for NEP is and PgC for land organic carbon change.



Fig. 5 Changes of vegetation carbon and soil organic carbon (SOC) in the northern high latitudes (NHL) in the Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) coupled simulations: (a) and (c) vegetation carbon; (b) and (d) SOC. Colored lines in (a) and (b) are for individual C4MIP models; in (c) and (d) the multimodel mean (black solid line) and the $\pm 1\sigma$ spread (gray shading) are shown. All changes are relative to 1901. A 6-year running mean is applied to all the curves. Units are in Pg C.

SOC pools. The difference between NPP and vegetation turnover is the net growth rate of vegetation carbon, and the difference between the vegetation turnover and SOM decomposition drives the net growth of SOC. The C4MIP models simulate a global total NPP of 54– 68 Pg C yr⁻¹ during 1901–1910 which lies within the range of observationally based estimates (Cramer *et al.* 1999, 2001). However, in the NHL region, C4MIP mod-

els differ significantly in the magnitude of simulated NPP which varies from 1.1 Pg C yr^{-1} in IPCC-CM4-LOOP to 6.8 Pg C yr^{-1} in UMD (2–13% of each model's global total). The C4MIP model-mean NPP in the NHL increases from 3.4 to 6.1 Pg C yr^{-1} by 2100, an 80% increase of vegetation activity (Fig. 6a). The IPSL-CM4-LOOP model even simulates more than a 400% increase in NPP. The model average vegetation-to-soil turnover rate is 2.5 Pg C yr^{-1} in the NHL (Fig. 6b). Higher biomass turnover is normally expected following more vegetation productivity. The difference of about 0.2 Pg C yr^{-1} remains in the vegetation and gets used during the growth phase (Fig. 6c). As a result, the sink of 17 Pg C is modeled, on average, to accumulate in the vegetation pool through 2100 as discussed before (Fig. 5c). The assumption that the biomass turnover is mostly proportional to NPP is reasonable because it is evident that more productivity can produce more biomass turnover, based on long-term observations.



Fig. 6 The multimodel mean and $\pm 1\sigma$ spread of carbon fluxes in vegetation in the northern high latitudes (NHL) in the Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) coupled simulations for: (a) net primary production; (b) vegetation turnover; (c) vegetation carbon growth rate. The changes are relative to the values of the year 1901; a 6-year running mean is applied to all the curves. Units are Pg C yr⁻¹ for all three panels.

The growth rate of SOC content is determined by the difference between vegetation turnover and SOM decomposition [Eqn (2)]. The mean of C4MIP models for these two factors is shown in Fig. 7. The NHL SOM decomposition is simulated to be greatly enhanced from 3.4 to 5.8 Pg C yr^{-1} by the warming (Fig. 7a); however, the SOM decomposition rate is smaller than the vegetation turnover rate, leading to carbon accumulation in soil (Fig. 7b). The C4MIP model-mean growth rate of the SOC increases until 2060, after which it decreases till 2100. This 'leveling-off' occurs because the SOM decomposition rate increases rapidly at higher temperatures and then catches up with the input from vegetation turnover. As the warming intensifies further, there is a possibility that the NHL soil in the C4MIP models could lose carbon after 2100, even if it does not do so in the 21st century as suggested by previous studies (Davidson et al., 2006). Indeed, one of the 10 C4MIP models (FRCGC) loses SOC toward the end of the 21st century, while three to four other models have their stopped increase. The above analysis suggests that the vegetation turnover contribution to SOC is of great significance in delaying SOC release due to warming in the NHL.

CO_2 fertilization vs. warming

Two major contributing factors have been identified as most important for stimulating high latitude vegetation growth: CO_2 fertilization and warming. The tundra and taiga vegetation in the NHL consist of C3 plants, which have shown higher productivity under elevated CO_2 conditions in lab and field experiments (Curtis & Wang,



Fig. 7 Same as Fig. 6 but for the changes of carbon fluxes in soil for: (a) heterotrophic respiration; (b) soil organic carbon (SOC) growth rate.

1998). Additionally, the ongoing and projected warming in the NHL has the potential to stimulate vegetation activity because growth in these regions is currently primarily limited by temperature (Nemani *et al.*, 2003).

To separate these two effects in the C4MIP models, we followed a method described in Friedlingstein et al. (2006). First, a scatter plot of modeled NPP vs. CO₂ in the uncoupled simulation was used to extract the model's strength of CO₂ fertilization (Fig. 8a and b). Since in the uncoupled simulation climate does not change (no long-term warming except internal variability), the change in NPP is driven mostly by CO₂ fertilization. Instead, since the NPP in the coupled simulation responds both to CO₂ increase and warming, the warming effect on NPP was obtained by subtracting the NPP in the uncoupled run from that of the coupled run (Fig. 8c and d). This method is only approximate as it neglects nonlinear effects, but it is the best way to extract such information with the two simulations provided.

An interesting feature is that while CO_2 fertilization effect enhances NPP everywhere [both globally and for high latitude regions (Fig. 8a and b)], the NPP response to temperature has the opposite sign for the global total and the NHL. In the NHL, NPP increases at higher temperature, in contrast to the adverse effect of climate change on vegetation productivity on global scale, which is dominated by changes in the mid-latitudes and the tropics (Friedlingstein *et al.*, 2006; Fig. 8c and d). Thus, despite the uncertainty in the strength of the CO_2 fertilization effect (Field, 2001) the increase in NPP in the NHL is robust.

The role of carbon cycle–climate feedback

Our analysis has so far used the fully coupled carbon cycle–climate simulations from the C4MIP models. A central finding of the C4MIP project is that the carbon cycle–climate feedback amplifies global warming, adding an additional global mean temperature increase of



Fig. 8 The sensitivity of net primary production (NPP) to CO_2 fertilization and temperature change for the global land (a, c) and the northern high latitudes (NHL) region (b, d) for the 10 Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) models. The NPP sensitivity to CO_2 fertilization (a, b) is calculated from the C4MIP uncoupled simulations, in which the climate is constant (preindustrial) while CO_2 increases for photosynthesis. Then NPP sensitivity to CO_2 fertilization at $2 \times CO_2$ is used in the coupled simulations to derive the NPP sensitivity to temperature increase. The NPP sensitivity to temperature in (b, d) thus is not the NPP directly from C4MIP-coupled simulation, but 'corrected' with NPP sensitivity to CO_2 fertilization from the uncoupled simulation. For details, refer to Friedlingstein *et al.* (2006).

0.1–1.5 °C and an additional CO₂ amount of 20–200 ppm (Friedlingstein *et al.*, 2006). Here, we examine the effect of this feedback on NHL carbon storage change by looking at the difference between the fully coupled runs and the uncoupled runs. The details of these runs are described in 'Models, data, and methodology' and Friedlingstein *et al.* (2006).

The additional effects of carbon cycle–climate feedback can also be seen through the two key factors, CO₂ fertilization and warming. The changes of vegetation carbon and of SOC in the NHL, as well as that for the whole globe are shown in Fig. 9. In contrast to the global scale in which the land reduces its capacity to take up carbon (Fig. 9a), the majority of the models simulate an increase in the ability of the land to take up carbon in the NHL due to carbon–climate feedback (Fig. 9b). All models show a robust increase in the vegetation carbon pool size in the NHL (Fig. 9d). This is not surprising since the carbon–climate feedback tends to exacerbate global warming and CO₂ increase. In contrast to the robust loss of SOC due to carbon cycle–climate feedback at the global scale in all C4MIP models (Fig. 9e), the NHL SOC response to climate feedback varies substantially in the models (Fig. 9f). Some models simulate a reduction in SOC in the NHL. However, the robust increase of NHL vegetation carbon (Fig. 9d) largely compensates for this carbon loss, resulting in a general net increase in the terrestrial carbon pool in the NHL. Further analysis (not shown) indicates that this is also caused by the increase of biomass turnover into soil as discussed above.

Discussion

The terrestrial ecosystems in the NHL cover 13% of the total global land area and consist mainly of boreal



Fig. 9 Differences in carbon storage during 1901–2100 between the coupled and uncoupled runs for the 10 Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) models for the global land total (a, c, e) and the northern high latitudes (NHL) (b, d, f); showing the additional effects due to carbon cycle–climate feedback. (a, b) total land organic carbon; (c, d) vegetation carbon; (e, f) SOC. All values are relative to the year of 1901. A 6-year running mean is applied to all the curves.

forests and tundra. During the past decades, a greening and vegetation migration accompanying the warming in the NHL have also been documented (Myneni et al., 1997; Zhou et al., 2001; Lloyd et al., 2003; Stow et al., 2004; Callaghan et al., 2005; Tape et al., 2006). The increase in terrestrial carbon due to CO₂ fertilization and warming counteracts some of the release of carbon from the enhanced organic matter decomposition. The warming in the future will accelerate the decay of the organic matter in the soil subsequently leading to CO₂ release to the atmosphere. It is even less clear how the vegetation photosynthesis and the SOM decomposition compete with each other when spatio-temporal patterns are taken into account. We used a suite of 10 fully coupled carbon climate simulations from C4MIP models to investigate the NHL terrestrial organic carbon uptake through the year 2100. Unlike many modeling studies using climate projections to solely force the carbon cycle models (McGuire et al., 2000; Cramer et al., 2001), the C4MIP coupled simulations consider the interactions between the carbon cycle and the climate, especially the feedback on the ecosystems (Friedlingstein et al., 2006). The models have large scatter and uncertainties, but unfortunately model details needed for pinpointing these uncertainties are not available. We nonetheless quantify the uncertainty by analyzing the model scattering using standard variance, as plotted in most of the model figures as shading. Although the current C4MIP model standard output limits us to quantify the similarities and differences of physical scheme across the models, our analysis of these C4MIP model results provides an insight into the carbon exchange between the vegetation and soil in the NHL and highlights the critical role of carbon cycleclimate interactions under global warming. Our findings affirm the prediction of continued enhanced vegetation growth under recent and future climate change, also described by many previous studies. However, it also reveals a rarely highlighted mechanism, namely that the increased vegetation turnover input to the SOC may drive an increase of the SOC pool, which could counter the loss of SOC in response to warming. In contrast to previous estimates that the future NHL soils will lose carbon due to warming (Davidson et al., 2006), our analysis of the C4MIP models indicate that the NHL soil can still continue to be a carbon sink until 2100. We estimate that NPP will increase by about 80% by 2100 in the NHL. The warming in the NHL region projected from C4MIP models does enhance SOC decomposition, which would otherwise drain SOC; however, high vegetation turnover from the enhanced vegetation productivity offsets the input to the soil and more than compensates for this additional SOM decomposition in the early 21st century. Davidson et al. (2006) discussed that terrestrial carbon models mostly use Q_{10} or Arrhenius equation for the SOM decomposition dependence on temperature. In both parameterizations, the decomposition rate has an exponential dependence on temperature, and this is why heterotrophic respiration accelerates at higher temperatures. Therefore, after 2060, the growth rate of NHL SOC begins to decrease because the SOM decomposition accelerates at higher temperature and catches up with the biomass turnover input. Thus, there is a possibility that the NHL soil may lose carbon by intense warming only after 2100, rather than in the 21st century. Vegetation biomass turnover is thus of great importance in linking vegetation carbon and SOC change in the near term.

Our analysis indicates that there are quite different underlying mechanisms that control global and NHL terrestrial carbon storage changes in these future projections. In contrast to the robust global land organic carbon loss generally projected to climate-carbon feedback, our analysis suggests that both CO₂ fertilization and the intense warming in the NHL may help enhance the terrestrial carbon sink there. An interesting point elucidated by the coupled carbon-climate feedback analysis is that on the global scale, the carbon loss from the ecosystem is dominated by SOM decomposition in the tropics, while the gain in the NHL is largely dominated by enhancement of vegetation productivity. Although the magnitude of the NHL terrestrial carbon pool and its change are much smaller than what is seen at the global scale, it is of major importance because of the continuing changes to the NHL terrestrial ecosystem under climate change. The projection of vegetation productivity enhancement is consistent with currently observed greening and a northward shift of vegetation distributions in the NHL.

Many off-line simulations also support this idea to varying extents. For instance, Cramer et al. (2001) suggested that the combination of CO₂ fertilization and climate change will enhance the terrestrial carbon uptake in the NHL by 2100. Schaphoff et al. (2006) modeled large areas of the boreal forest between 30 and 60° N as a CO₂ source in the future, while the high northern latitudes in Canada, and to a limited extent, some areas of the Siberian Arctic were projected to be a carbon sink by 2100. Sitch et al. (2007) found that the tundra is greening in the Arctic based on a 20-year data record of satellite data and pointed out that off-line simulations of process-based models generally agree that Arctic tundra will be a small carbon sink over the next century as enhanced vegetation production exceeds simulated increases in decomposition.

Not all potentially relevant processes have been considered in all the C4MIP models. This results in numerous uncertainties of the projected change of terrestrial carbon storage in the Arctic based on both the C4MIP simulations and offline simulations, such as changes in land use, response of insects to climate change, future evolution of fire regimes, carbon–nitrogen feedbacks, nonlinearities of the SOM decomposition rate with pool size, soil moisture–precipitation effects, and uncertainties relating to changes in the soil environment. Each of these effects will be discussed briefly below.

Related to these effects, a major caveat to the C4MIP simulations, and therefore to our conclusion of an increasing SOC pool, is that the carbon pools in the permafrost and peatland regions are not explicitly represented in these models. When the top soil layer of permafrost thaws in the future, much of the large substrate pool is likely to decompose quickly, and large amounts of carbon become available for decomposition (Goulden et al., 1998; Serreze et al., 2000; Khvorostyanov et al., 2008). As the NHL warms significantly, the warming-induced deepening of the layer of seasonal biological activity may cause a net loss of deep SOC in the boreal forest and tundra. We are unfortunately limited to the currently available C4MIP model results, and such possibilities can only be fully addressed in future models that better represent these processes.

Most C4MIP groups also have no fire components in their models. Future NHL warming may potentially lengthen the fire season and increase the probability of fires in boreal ecosystems (Randerson et al., 2006; Bond-Lamberty et al., 2007). Wildfires destroy most of aboveground biomass and consume organic soils, and increased fire activity could result in net loss of carbon to the atmosphere and a positive feedback to global climate change (Harden et al., 2000). In addition to direct combustion, ecological conditions for the microorganisms change greatly after wildfires and the indirect effect of wildfire on SOM decomposition is also unclear (Schimel and Gulledge, 1998). There have been observations of increased CO₂ fluxes in the short term due to elevated soil temperatures after fire (Richer et al., 2000; Bergner et al., 2004); however, lower heterotrophic respiration rates are also observed (Bond-Lamberty et al., 2004; Certini, 2005). The direct and indirect effects of wildfires are complex and were not considered in most C4MIP models.

Another potential factor is that the models do not consider the impacts of some natural disturbances, such as insects on the destruction of trees. For example, Kurz *et al.* (2008) has showed that insects such as the mountain pine beetles destroy trees particularly in the boreal forests of Canada thereby increasing the carbon emitted to the atmosphere.

Additionally, none of the C4MIP models included the effects of possible future land use and land cover change (Friedlingstein *et al.*, 2006). Besides tundra and

boreal forest, the NHL also includes large rivers and lakes, river floodplain ecosystems, and land use by agriculture. To date, the changes in agricultural land use in the NHL region have been small (Zhuang *et al.*, 2003). However, in the next century the effects of land-use and land cover changes in the NHL may become important for future biogeography and biogeochemistry.

Also of potential importance is the carbon-nitrogen feedback. CO₂ fertilization may be constrained by the availability of nutrients, particularly nitrogen (Nadelhoffer et al., 1999; Field, 2001; Hungate et al., 2003; Luo et al., 2004). Thus, inclusion of nitrogen could probably reduce the greening in the models. However, it can be expected that warming will also accelerate nitrogen mineralization in the soil and perhaps weakening the effects of nitrogen limitation. None of C4MIP models contains a full treatment of the nitrogen cycle (Friedlingstein et al., 2006). If CO₂ fertilization is not as strong as represented in most of these models, the vegetation productivity enhancement would be weaker, but it would still increase even for warming effect alone. For instance, the UMD model has the weakest CO₂ fertilization effect (Fig. 8a), yet projects a high vegetation carbon increase (Fig. 5a).

Besides temperature, precipitation is another important climatic factor for the vegetation growth in midlatitudes and the tropics (Zeng *et al.*, 2005a, b; Knorr *et al.*, 2007) as well as at high latitudes (Piao *et al.*, 2006; Schaphoff *et al.*, 2006; Sitch *et al.*, 2007). Moreover, the soil hydrology changes dramatically as permafrost thaws with warming (Jorgenson *et al.*, 2001). Soil moisture has been suggested to play an important role for constraining rates of decomposition (Post *et al.*, 1982; Qian *et al.*, 2008). Unfortunately, the current study does not investigate the effect of soil moisture on NHL ecosystems because no information of precipitation and soil content from C4MIP is provided in the standard output.

Lastly, it is known that the SOM decomposition is dependent on the SOC pool size itself. We have excluded this effect in our analysis because the NHL soil pool is modeled to increase only by about 8%, compared with the 74% increase of heterotrophic respiration.

Conclusion

The possibility of rapid loss of organic carbon in the northern high latitude regions under intense global warming is a major concern of climate change research. In this study, we used the C4MIP simulations to investigate the NHL terrestrial carbon storage from 1901 to 2100. The 10 C4MIP models projects a mean warming



Fig. 10 Conceptual diagram of effects of CO_2 fertilization and intense warming in the northern high latitudes (NHL) on the changes of carbon fluxes and storages by 2100 from Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) coupled simulations. The multimodel mean and 1 SD are provided to indicate the relative magnitudes of these changes. All changes are relative to 1901. The CO_2 and climate change (warming) are external forcings and are indicated in ellipses. Terrestrial carbon fluxes are indicated in rectangles and carbon pools are indicated in oval boxes. The multimodel 'Mean \pm SD' is provided for each variable Units are Pg C yr⁻¹ for carbon flux and Pg C for carbon storage.

of 5.6 °C from 1901 to 2100 in the NHL, in contrast to a mean global warming of 3.2 °C. The CO₂ fertilization and intense warming will impact the terrestrial organic carbon storage in the NHL. The mean of the C4MIP coupled simulations suggest that the NHL will be a carbon sink of size $0.3\pm0.3\,Pg\,C\,yr^{-1}$ by 2100. This net carbon sink in the NHL is caused by a mechanism wherein the terrestrial vegetation productivity is larger than the SOM decomposition in the high latitudes. This results in an increase of about $38 \pm 20 \text{ Pg C}$ land organic carbon between 1901 and 2100. Of this, the vegetation carbon pool increases by about $17 \pm 8 PgC$, and the SOC pool increases by about 21 ± 16 Pg C. A factor that has received relatively little attention is the vegetation turnover to soil which drives the modeled SOC increase despite of the higher decomposition rate. These results and mechanisms are summarized in Fig. 10. It is noted that several potentially important issues such as nutrient limitation to CO₂ fertilization, the effects of soil moisture on decomposition rate, and mechanistic representation of permafrost are either not adequately represented in the models or difficult to analyze given the limited model experiments that were performed.

Although the magnitude of vegetation carbon increase is somewhat smaller than that of the soil, it is a 43% increase, much larger than the 8% increase in the SOC pool. More importantly, all models agree on vegetation carbon increase because both CO₂ fertilization effect and warming lead to high vegetation productivity. In contrast, larger uncertainty exists in SOC change which is the result of the difference between increased vegetation turnover and enhanced SOC decomposition. Although most of the C4MIP models project a small SOC sink in the 21st century, the rate of SOC increase begins to level off after 2060 because SOM decomposition accelerates at high temperatures and then catches up with the additional input from vegetation biomass turnover. We speculate that such competing mechanisms may lead to a switch of the NHL soil pool from a net carbon sink to source after 2100. If CO₂ fertilization effect is not as strong as parameterized in these models, this switch may take place earlier.

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