Modelling 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

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Abstract

We are developing a process-based modelling approach to investigate how carbon (C) storage of tundra across the entire Arctic will respond to projected climate change. To implement the approach, the processes that are least understood, and thus have the most uncertainty, need to be identified and studied. In this paper, we identified a key uncertainty by comparing the responses of C storage in tussock tundra at one site between the simulations of two models – one a global-scale ecosystem model (Terrestrial Ecosystem Model, TEM) and one a plot-scale ecosystem model (General Ecosystem Model, GEM). The simulations spanned the historical period (1921–94) and the projected period (1995–2100). In the historical period, the model simulations of net primary production (NPP) differed in their sensitivity to variability in climate. However, the long-term changes in C storage were similar in both simulations, because the dynamics of heterotrophic respiration (R_H) were similar in both models. In contrast, the responses of C storage in the two model simulations diverged during the projected period. In the GEM simulation for this period, increases in R_H tracked increases in NPP, whereas in the TEM simulation increases in R_H lagged increases in NPP. We were able to make the long-term C dynamics of the two simulations agree by parameterizing TEM to the fast soil C pools of GEM. We concluded that the differences between the long-term C dynamics of the two simulations lay in modelling the role of the recalcitrant soil C. These differences, which reflect an incomplete understanding of soil processes, lead to quite different projections of the response of pan-Arctic C storage to global change. For example, the reference parameterization of TEM resulted in an estimate of cumulative C storage of $2032\,\mathrm{g\,C\,m^{-2}}$ for moist tundra north of 50°N, which was substantially higher than the $463\,\mathrm{g\,C\,m^{-2}}$ estimated for a parameterization of fast soil C dynamics. This uncertainty in the depiction of the role of recalcitrant soil C in long-term ecosystem C dynamics resulted from our incomplete understanding of controls over C and N transformations in Arctic soils. Mechanistic studies of these issues are needed to improve our ability to model the response of Arctic ecosystems to global change.

Keywords: carbon storage, climate change, general ecosystem model, net ecosystem production, terrestrial ecosystem model, tundra ecosystems.

Introduction

The Intergovernmental Panel on Climate Change (IPCC) has concluded that the build-up of greenhouse gases in the atmosphere is likely to lead to mean annual global

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temperature increases of between 1.0 and 3.0 °C by 2100 (IPCC 1996) with larger increases occurring at high latitudes (Hansen & Lebedeff 1987; Lashof & Ahuja 1990). There is evidence that warming is occurring in some high-latitude areas (Beltrami & Mareschal 1991; Chapman & Walsh 1993), and that the warming may be affecting both the function and structure of Arctic ecosystems (Oechel *et al.* 1993, 1995; Chapin *et al.* 1995). Functional responses represent changes in the biogeo-chemical cycling of carbon (C), nutrients, and water in ecosystems, while structural responses represent changes in the species composition across a landscape, and may further modify the function of ecosystems (Melillo *et al.* 1996a). Changes in ecosystem structure and function in response to global change may influence the C storage capacity of Arctic tundra.

Tundra ecosystems contain approximately 11% of the world's soil C that might react to near-term climate change (McGuire *et al.* 1995a; Melillo *et al.* 1995; McGuire & Hobbie 1997). A substantial amount of C and nitrogen (N) could be released in inorganic forms as these soils warm, the active layer deepens, decomposition rates increase, and the growing season lengthens (Nadelhoffer *et al.* 1991). A large release of carbon dioxide (CO_2), from these soils has the potential to increase atmospheric CO_2, which in turn may enhance the rate and magnitude of climate change (i.e. a positive feedback). However, a large release of inorganic N from organic matter may also result in increased net primary production (NPP; Shaver *et al.* 1992). This response has the potential to buffer the C loss from the soil or cause Arctic ecosystems to act as a net sink for atmospheric CO_2 (i.e. a negative feedback).

McGuire *et al.* (2000) used a global-scale ecosystem model, the Terrestrial Ecosystem Model (TEM), to evaluate the potential sensitivity of simulated C storage in Arctic tundra to temporal and spatial variation in historical and projected climate across the pan-Arctic from 1921 to 2100. In these simulations, C storage of tundra increases substantially across the pan-Arctic during the projected period. However, these model estimates represent the suite of assumptions about the function and structure of tundra ecosystems in the Arctic that have been incorporated into TEM. The results of the simulation need to be evaluated in the context of uncertainties associated with (1) the climate data sets used as drivers (2) the ability to represent vegetation heterogeneity and dynamics (3) the ability to represent topographic controls over C storage, and (4) the representation of ecological processes, such as photo-synthesis and decomposition. Compared with plot-scale ecosystem models, ecological processes in global-scale ecosystem models are generally represented in a simpler fashion. In this study we focus on evaluating the implications of uncertainty in the representation of ecological processes in TEM for the long-term responses of pan-Arctic C storage.

Differences in the representation of ecosystem pro-cesses by ecosystem models may be caused by the following: (1) different conceptualizations of the relation-ships among ecosystem processes, different formulations of the same ecosystem processes, and different para-meterizations of the same formulations (McGuire *et al.* 1997; Cramer *et al.* 1999; Jenkins *et al.* 1999); (2) the use of different input data sets (Pan *et al.* 1996); (3) application of the models at different spatial resolutions (Jenkins *et al.* 1999; Nungesser *et al.* 1999); or (4) the use of different simulation protocols in applying the models. To identify process-based uncertainties related to differences in conceptualization, formulation, and parameterization among models, it is necessary to minimize differences associated with other sources by standardizing input data sets and simulation protocols, which is a standard practice in formal comparisons among models (McGuire *et al.* 1993; VEMAP Members 1995; Heimann *et al.* 1998; Cramer *et al.* 1999; Jenkins *et al.* 1999; Kicklighter *et al.* 1999; Schimel *et al.* 2000).

In this study, we compare the responses of TEM with the responses of the General Ecosystem Model (GEM; Rastetter *et al.* 1991) to identify how the representation of processes influences the long-term C dynamics of the two models. The GEM, which is a plot-scale ecosystem model that has been parameterized extensively with informa-tion from field studies at Toolik Lake, AK, has been used to evaluate historical and projected responses of C storage in tussock tundra at Toolik Lake (McKane *et al.* 1997a, 1997b; Hobbie *et al.* 1998). Our strategy is to run both models with the same inputs at Toolik Lake so that we can isolate the processes responsible for differences in the long term dynamics of C storage simulated by the models. We focus this comparison at Toolik Lake, because, over the past decade, there have been many process studies of tussock tundra conducted at the Toolik Lake field site in Alaska (Shaver & Chapin 1986, 1991; Oechel & Riechers 1987; Grulke *et al.* 1990; Shaver *et al.* 1990; Giblin *et al.* 1991; Oechel *et al.* 1992; Chapin *et al.* 1995). Some of these experiments have examined ecosystem responses to perturbations of elevated atmo-spheric CO_2 (Oechel & Riechers 1987; Grulke *et al.* 1990; Oechel *et al.* 1992), N fertilization, greenhouse warming, and shading (Chapin *et al.* 1995). Both GEM and TEM have used some of these studies in parameterizing the biogeochemical dynamics of tussock tundra, and they both quantitatively reproduce the decadal responses observed in the experiments (McKane *et al.* 1997a, 1997b; this paper). After comparing the models to isolate the processes responsible for differences in long-term C dynamics between the models, we then modify TEM

based on the processes identified, verify the dynamics of C storage simulated by TEM, and then examine the implications for long-term responses of pan-Arctic C storage simulated by the model.

Methods

Overview

Because of the wealth of process-based data at Toolik Lake, we compare the simulated C dynamics between GEM and TEM for historical and projected climate inputs associated with the Toolik Lake field site. It is possible to standardize the inputs for GEM and TEM because the models have similar input requirements. Because we are interested in the pan-Arctic implications of process-based differences between the models, we compare the long-term responses of C storage simulated by GEM and TEM for tussock tundra of the Toolik Lake study area using the climate extracted from the gridded data sets used in the pan-Arctic study of McGuire et al. (2000). Our strategy of comparing the performance of the models driven with the same inputs for a well-studied field site derived from a global data set allows us to (1) isolate the processes responsible for differences (2) modify TEM based on the processes identified as being responsible for the differences in long-term C dynamics between the models (3) verify the dynamics of C storage simulated by the modified model, and (4) examine the implications for long-term responses of pan-Arctic C storage. Below, we briefly describe the versions of GEM and TEM, the input data sets, and the simulation protocol used in this study.

Model descriptions

GEM. The GEM is a process-based, plot-scale, lumped-parameter model of the interaction of C and N in terrestrial ecosystems (Rastetter et al. 1991). It calculates ecosystem responses to changes in atmospheric CO_2 concentrations, temperature, soil moisture, irradiance, and inorganic N inputs to the ecosystem. The GEM has been used in several studies to examine responses to global change in Arctic tundra (Rastetter et al. 1991; Rastetter 1996; McKane et al. 1997a, 1997b; Hobbie et al. 1998) and other ecosystems (Rastetter et al. 1991; McKane et al. 1995).

The GEM simulates stand-level photosynthesis and N uptake by plants, allocation of C and N to leaves, stems, and fine roots, respiration of these tissues, turnover of biomass through litterfall, and decomposition of that litter in soils (Fig. 1). Carbon dioxide is lost from the ecosystem through plant respiration and soil decomposition; inorganic N is lost through a process which is assumed to be proportional to inorganic N concentra-
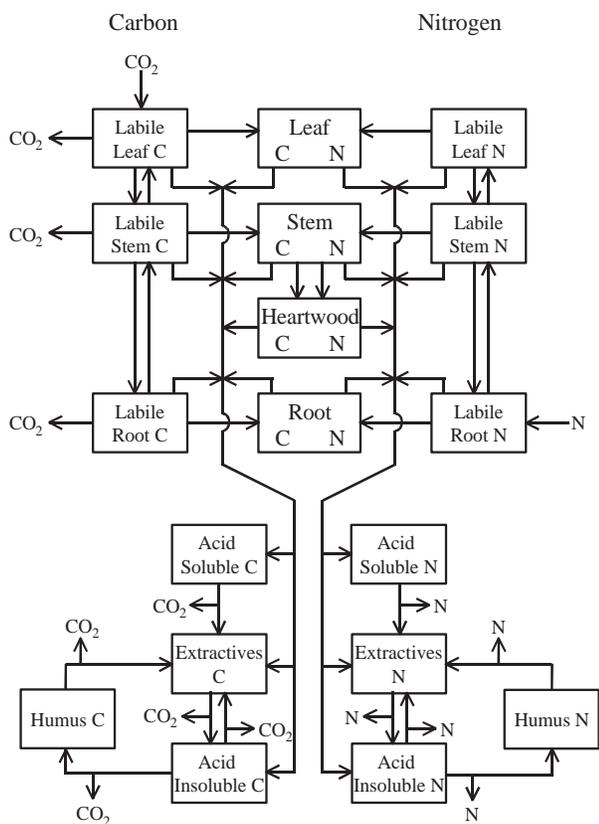
tions in the soils. The GEM has a time step of one year; it is calibrated to use the mean climate of the growing season to simulate annual C dynamics.

A major feature of GEM is the adaptation of vegetation to maintain a nutritional balance between C and N as the environment changes. Changes that stimulate photosynthesis (such as increased CO_2 concentration) cause an increase in allocation of C and N to fine roots to stimulate N uptake. Similarly, an increase in inorganic N will increase allocation of C and N to foliage, which will then enhance C uptake. Through the coupling between C and N uptake by plants, the model incorporates biogeochemical constraints of the N cycle on C dynamics.

For the application of GEM to tundra ecosystems, we used the implementation described in several publications (McKane et al. 1997a, 1997b; Rastetter et al. 1997; Hobbie et al. 1998). Briefly, the model was calibrated to biomass and production of moist acidic tussock tundra based on a 9-year study reported by Chapin et al. (1995) in which vegetation plots at Toolik Lake, AK, were experimentally manipulated with fertilizer, greenhouses, and shade houses. Results from an experiment that doubled atmospheric CO_2 in chambers at the same site (Oechel et al. 1992) were also used to calibrate the model. The calibration procedure resulted in a single parameter-set that is simultaneously consistent with the responses of all these experimental manipulations. The application of GEM with this parameter set successfully reproduces the responses observed in the experiments of Chapin et al. (1995; see Fig. 2a) and Oechel et al. (1992; see Fig. 3).

TEM. The TEM is a process-based, global-scale ecosystem model that uses spatially referenced information on climate, elevation, soils, and vegetation to make monthly estimates of important C and N fluxes and pool sizes of the terrestrial biosphere (Fig. 4). In this study we apply TEM to a single grid cell at Toolik Lake and use version 4.1 of the model (McGuire et al. 1997; Tian et al. 1999), which is a version that has been applied to evaluate responses of terrestrial ecosystems to historical and projected changes in atmospheric CO_2 and climate for the globe (Melillo et al. 1996a, 1996b; Xiao et al. 1998; Kicklighter et al. 1999), the Amazon River Basin (Tian et al. 1998), and the conterminous United States (Tian et al. 1999). Version 4.1 of TEM has been applied to evaluate the sensitivity of C responses of pan-Arctic tundra ecosystems to spatial and temporal variation in climate (McGuire et al. 2000) and to evaluate whether consideration of the effects of snowpack on winter decomposition would improve the ability of the model to simulate the seasonal cycle of atmospheric CO_2 at high latitude monitoring stations (McGuire et al. 1999). In this study, we apply the version of TEM used in McGuire et al. (2000).

TEM simulates most of the processes represented in GEM and uses many of the same driving variables. In comparison with GEM, TEM represents vegetation and soil pools in a more aggregated fashion. The simpler structure of TEM provides the computational efficiency necessary to apply the model to simulate continental-and global-scale responses of terrestrial ecosystems in a spatially explicit manner. Although the model does not explicitly allocate C and N among plant tissues, the formulations of vegetation processes in TEM implicitly allocate effort to C and N uptake based on an assessment of C-N balance of the vegetation (McGuire *et al.* 1992; Pan *et al.* 1998). Simulations with TEM indicate that N control of C assimilation is especially strong in high latitudes (McGuire *et al.* 1992; Melillo *et al.* 1993); this control has been experimentally demonstrated in numerous studies (Van Cleve & Zasada 1976; Shaver & Chapin 1980, 1986; Chapin *et al.* 1986; Chapin 1991). Similarly, although the model does not track separate pools of soil organic matter, the formulations in the model implicitly consider issues of C quality and turnover (McGuire *et al.* 1995a, 1997). Simulations of C storage responses in high latitudes by TEM are sensitive to assumptions about how increases in atmospheric CO_2 influence tissue chemistry and the decomposition of soil organic matter (McGuire *et al.* 1997).

The application of TEM for simulating C dynamics requires the use of the monthly climatic data and the soil- and vegetation-specific parameters appropriate to the
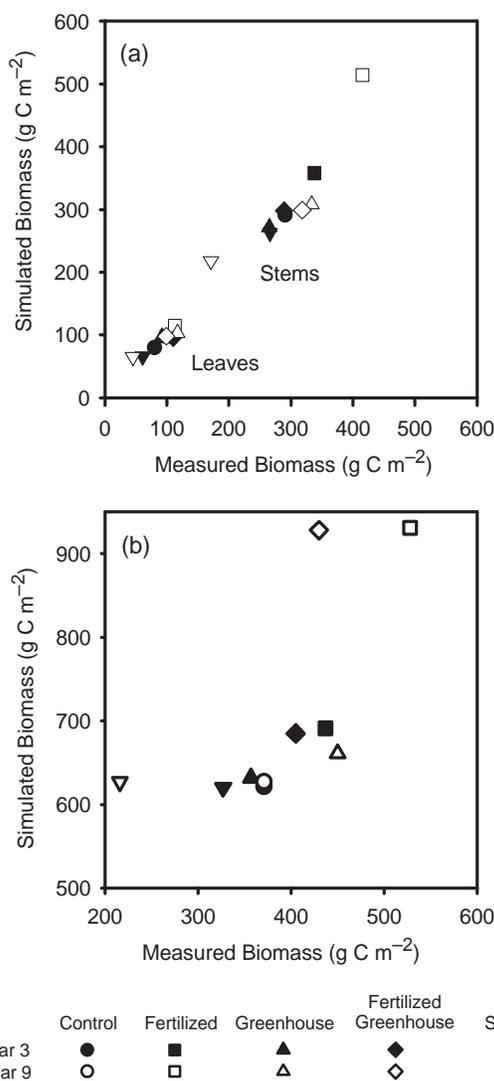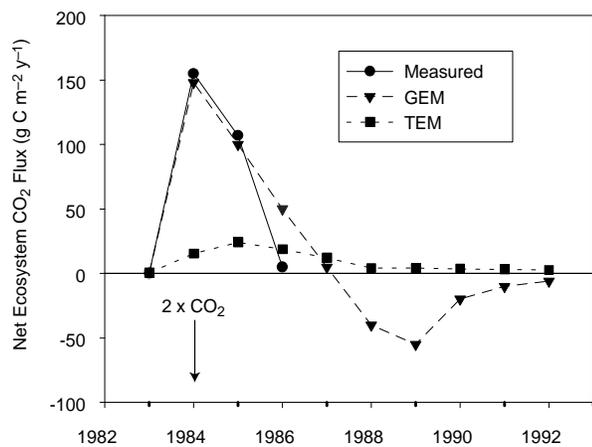

Fig. 2 Measured vs. simulated responses of tussock tundra at Toolik Lake to fertilized, greenhouse, fertilized greenhouse, and shaded treatments of Chapin *et al.* (1995) for (a) GEM (adapted from Figs 1 in McKane *et al.* 1997b) and (b) TEM. The fertilized treatments received $10\,g\,N\,m^{-2}$ per year as NH_4NO_3 and $5\,g\,P\,m^{-2}$ per year as triple superphosphate. The greenhouse treatments increased mean growing-season temperature by $3.5\,°C$. The shaded treatment decreased light by 50% of ambient. In (b), measured biomass is the sum of leaves and stems, and simulated biomass by TEM is the sum of leaves, stems and roots.

Fig. 1 Schematic diagram of Marine Biological Laboratory GEM, a general ecosystem model of C and N cycles within terrestrial ecosystems. Equations for processes are given in Rastetter *et al.* (1991).

soil and vegetation of the spatial unit under consideration. Although many of the parameters are defined from published information, some are determined by calibrating the model to fluxes and pool sizes of intensively studied field sites. For the application of TEM to tundra ecosystems in this study, we calibrated TEM to the fluxes and pools of moist tundra for the Toolik Lake study site (see Table A2 in McGuire *et al.* 1992). The parameter that controls N losses from the model was calibrated so that simulated losses at equilibrium are $0.06\,g\,N\,m^{-2}$ per year in response to atmospheric N inputs of the same level, which is equivalent to N inputs measured at Toolik Lake (McKane *et al.* 1997b).

Information from several studies of C dynamics in Arctic tundra have been incorporated into our para-

meterization for tussock tundra (Chapin *et al.* 1980; Shaver & Chapin 1986, 1991; Shaver *et al.* 1990; Giblin *et al.* 1991). For the input variables associated with the Toolik Lake grid cell, TEM quantitatively reproduces the measured biomass changes that have been observed in Chapin *et al.* (1995; see Fig. 2b). Note that the over-estimate by TEM in Fig. 2(b) is expected, because the aggregated biomass simulated by TEM includes leaves, stems and roots, and the experiment only measured leaves and stems. Although the short-term response simulated by TEM to an instantaneous doubling of atmospheric CO_2 does not reach the values observed in the experiment of Oechel *et al.* (1992), the long-term response of the model is similar to the acclimation observed in the experiment (Fig. 3).

Input data sets and simulation protocol

The simulation of C dynamics for tussock tundra at the Toolik Lake field site from 1921 to 2100 required that we organize a number of input data sets for both models (Table 1). To simulate the influence of N inputs, we added $0.06\,g\,N\,m^{-2}$ each year to the inorganic N pool of each model. This level of N input is equivalent to N inputs measured at Toolik Lake (McKane *et al.* 1997b). In GEM, N inputs are added annually, while in TEM, N inputs are added monthly based on the monthly proportion of annual soil water recharge from snowmelt and rain. In TEM, elevation was 559 m and soil texture was 80% sand, 10% silt, and 10% clay.

Mean monthly cloudiness in this study is calculated as 100% minus the per cent monthly sunshine duration from the CLIMATE data base (see Cramer *et al.* 1999), which is a major update of the data set described in Leemans & Cramer (1991). Development of this data set is described in detail in McGuire *et al.* (2000). Based on monthly cloudiness, TEM simulates monthly PAR, which is a driving variable for the gross primary productivity formulation of TEM. Because GEM requires data on

Fig. 3 Measured vs. simulated short-term change in net ecosystem flux of tussock tundra at Toolik Lake in response to an instantaneous increase in atmospheric CO_2 from $344\,\mu L\,L^{-1}$ (ambient) to $680\,\mu L\,L^{-1}$. The CO_2 treatment was maintained for three consecutive growing seasons as described by Oechel & Riechers (1987), Grulke *et al.* (1990), and Oechel *et al.* (1992). Data represent mean differences between treatment and ambient fluxes. Positive fluxes indicate C storage. Data from GEM adapted from Fig. 2 in McKane *et al.* (1997a).

Table 1 Input variables for GEM and TEM simulations: description of temporal resolution and scope of each variable

| Variable	Temporal resolution	Temporal scope	GEM	TEM
Vegetation	Constant	–	Yes	Yes
Nitrogen inputs	Constant	–	Yes	Yes
Atmospheric CO_2	Semi-annual	1921–2100	Yes	Yes
Elevation	Constant	–	No	Yes
Soil texture	Constant	–	No	Yes
Cloudiness	Month	Long-term mean	No	Yes
PAR	Month	Long-term mean	Yes	No
Temperature	Month	1921–2100	Yes	Yes
Precipitation	Month	1921–2100	No	Yes
Soil moisture	Month	1921–2100	Yes	No
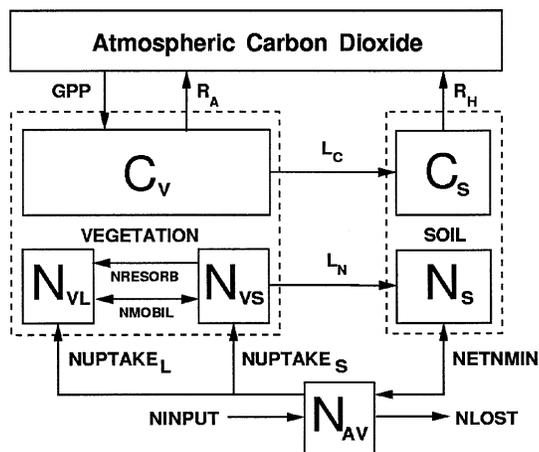
Fig. 4 The TEM. The state variables are as follows: carbon in the vegetation (C_V); structural N in the vegetation (N_{VS}); labile N in the vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic N in soils and detritus (N_S); and available soil inorganic N (N_{AV}). Arrows show C and N fluxes; GPP, gross primary production; R_A, autotrophic respiration; R_H, heterotrophic respiration; L_C, litterfall carbon; L_N, litterfall N; NUPTAKE$_S$, N uptake into the structural N pool of the vegetation; NUPTAKE$_L$, N uptake into the labile N pool of the vegetation; NRESORB, N resorption from dying tissue into the labile N pool of the vegetation; NMOBIL, N mobilized between the structural and labile N pools of the vegetation; NETNMIN, net N mineralization of soil organic N; NINPUT, N inputs from outside the ecosystem; and NLOST, N losses from the ecosystem.

growing season PAR, we aggregated monthly PAR simulated by TEM for the three growing season months (June–August) to create a PAR data set for GEM.

Historical and projected atmospheric CO_2 are as described in McGuire *et al.* (2000). Historical and projected temperature and precipitation for the Toolik Lake grid cell were extracted from the gridded data set that was used by McGuire *et al.* (2000), which has a spatial resolution of $0.5° \times 0.5°$ (latitude $\times$ longitude). To standardize soil moisture between the models, we used TEM to simulate monthly soil moisture as per cent water-filled-pore-space (% WPFS) from 1920 to 2100 based on the historical and projected data sets of monthly temperature and precipitation. From the monthly data set of WFPS, we aggregated % WFPS for the three growing season months to create a data set of soil moisture for GEM.

During the historical period, the mean annual temperature of the Toolik Lake grid cell varies within approximately 2° of –8 °C (Fig. 5a). The mean growing season temperature varies within approximately 2° of 11 °C (Fig. 5a). By the end of the projected period, both mean annual and mean growing season temperatures have increased 4–5 °C (Fig. 5a). At the beginning of the
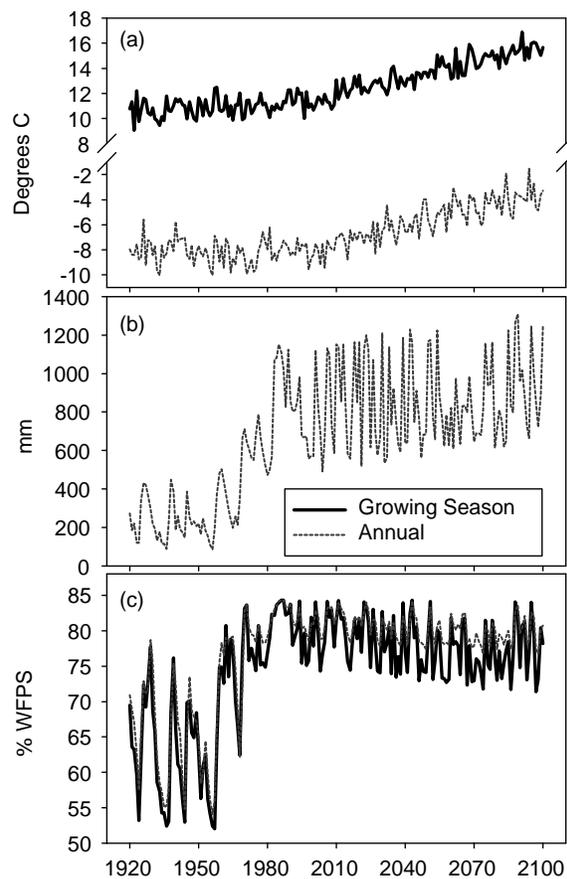
Fig. 5 Historical and projected mean growing season and mean annual (a) air temperature, (b) precipitation and (c) soil moisture for the Toolik Lake grid cell.

historical period, annual precipitation of the Toolik Lake grid cell varies between approximately 100 mm per year and 500 mm per year until the 1970s, at which time it increases gradually to approximately 1000 mm per year by the end of the historical period (Fig. 5b). Throughout the projected period, precipitation of the Toolik Lake grid cell varies between approximately 600 mm per year and 1200 mm per year. At the beginning of the historical period, soil moisture (both annual and growing season) of the Toolik Lake grid cell varies between approximately 55% and 80% WFPS until the 1970s, when mean growing season soil moisture fluctuates between 80% and 85% WFPS, which it continues to do throughout the projected period. After the 1970s and through the projected period, mean annual soil moisture fluctuates between 80% and 85% WFPS exhibiting less variation than displayed in the growing season values (Fig. 5c). As discussed by McGuire *et al.* (2000), there are substantial uncertainties in the grid-based temperature and precipitation data sets that have been developed for the pan-Arctic, because the density of weather stations is low. In

particular, there are substantial problems with grid-based precipitation data sets, because few reliable precipitation data are available. Although some of the historical variability in precipitation is likely an artifact of the low station density and changing methodology through time for the measurement of precipitation, the variability in the precipitation data set allows us to compare and evaluate the dynamics of the models more fully.

To initialize the simulations, we ran each of the models to equilibrium using the average climate for the period from 1921 to 1930, which was calculated as the mean monthly temperature and precipitation for each month from 1921 through 1930. For each model, the equilibrium pools of C and N in soils and vegetation estimated for this mean climate were used as the initial conditions for simulating the temporal dynamics of C storage from 1921 to 2100.

Results

Simulated carbon dynamics for historical climate

Net primary production. The equilibrium estimates of NPP for the Toolik Lake grid cell at the beginning of the simulation are similar for both models (GEM, $124\,g\,C\,m^{-2}$ per year; TEM, $127\,g\,C\,m^{-2}$ per year). Throughout the historical period, NPP estimated by GEM oscillates with a period of approximately 10 years (Fig. 6a). This oscillation is centred around $100\,g\,C\,m^{-2}$ per year until 1969, at which time NPP starts to decrease and reaches approximately $90\,g\,C\,m^{-2}$ per year by 1994. The temporal variation of simulated NPP is associated with the temporal variation in the precipitation and soil moisture (Figs 5b,c), which oscillate with a period of approximately 10 years and increase in 1969. In contrast to GEM, the variability of NPP estimated by TEM is primarily interannual, and tends to be centred around $130\,g\,C\,m^{-2}$ per year throughout the historical period.

Heterotrophic respiration. The equilibrium estimates of heterotrophic respiration (R_H) at the beginning of the simulation are similar for both models (GEM, $124\,g\,C\,m^{-2}$ per year; TEM, $127\,g\,C\,m^{-2}$ per year). Similar to NPP, historical R_H estimated by GEM oscillates with a period of approximately 10 years, is centred around $120\,g\,C\,m^{-2}$ per year until 1969, and decreases between 1969 and 1994 (Fig. 6b). Thus, the variation in R_H is also associated with the variation in precipitation and soil moisture. In contrast to NPP, variation in R_H estimated by TEM is very similar to variation estimated by GEM (Fig. 6b, $r^2 = 0.83$). Thus, R_H is tightly coupled to soil moisture in

both models (Table 2). For the historical period, net N mineralization (NMIN) is tightly coupled to R_H in the GEM simulation, but not in the TEM simulation (Table 2).

Net ecosystem production. The estimates of net ecosystem production (NEP), which is the difference between NPP and R_H, are approximately zero for both models at the beginning of the simulation (GEM, $-0.02\,g\,C\,m^{-2}$ per year; TEM, $-0.3\,g\,C\,m^{-2}$ per year). These estimates indicate that the models are in equilibrium prior to simulating historical C dynamics. For the historical period, GEM estimates that mean C storage of tussock tundra at Toolik Lake decreased by $-5.3\,g\,C\,m^{-2}$ per year, while the TEM simulation estimates a slight increase of $2.8\,g\,C\,m^{-2}$ per year. The difference in C storage is primarily associated with differences in simulated C dynamics after 1969. Between 1921 and 1969, the variation in NEP estimated by both models tends to track variation in simulated R_H (Fig. 6c). After 1969 both NPP and R_H estimated by GEM decrease by a similar amount, so that the variation in simulated NEP fluctuates around $4\,g\,C\,m^{-2}$ per year. In contrast, the estimates of NPP by TEM after 1969 are relatively stable while R_H decreases, so that NEP fluctuates around $40\,g\,C\,m^{-2}$ per year.

Cumulative change in carbon storage. Both models estimate similar cumulative changes in vegetation C throughout the historical period, although GEM shows a slight decrease from the 1960s until the end of the historical period (Fig. 7a). Both models also estimate similar cumulative changes in soil C, although TEM shows more of a decrease in the middle of the historical period than GEM (Fig. 7b). Cumulative changes in ecosystem C, which is the sum of changes in vegetation C and soil C, reflects the cumulative changes in soil C throughout the historical period for both models (Fig. 7c).

Simulated carbon dynamics for projected climate

Net primary production. Both models estimate that NPP of tussock tundra at the Toolik Lake study area increases over the course of the projected period (Fig. 6a). Although NPP estimated by GEM at the beginning of the projected period (approximately $100\,g\,C\,m^{-2}$ per year) is lower than NPP estimated by TEM (approximately $139\,g\,C\,m^{-2}$ per year), NPP estimates are similar by the end of the projected period (approximately $150\,g\,C\,m^{-2}$ per year). In contrast to the historical period, NPP estimated by GEM in the projected period is weakly sensitive to soil moisture (Table 2). Similar to the historical period, the NPP estimates of TEM in the projected period are not sensitive to soil moisture (Table 2). The NPP estimates by both models in the projected period are sensitive to air temperature, which

Table 2 Proportion of variation explained by correlation of annual net primary production (NPP) and annual heterotrophic respiration (R_H) with other variables, including mean growing season (June–August) temperature, mean growing season soil moisture and annual net nitrogen mineralization (NMIN) for the GEM simulation and mean annual temperature, mean annual soil moisture and annual NMIN for the TEM simulation

		Historical period			Projected period		
		Air temperature	Soil moisture	NMIN	Air temperature	Soil moisture	NMIN
GEM	NPP	NC[1]	NC[1]	NC[1]	0.56	0.43	0.76
	R_H	NC[1]	0.83	0.95	0.68	0.57	0.97
TEM	NPP	NC[1]	NC[1]	0.25	0.47	NC[1]	0.42
	R_H	NC[1]	0.95	NC[1]	0.31	0.66	0.61

[1] No correlation, as evaluated by significance at the 0.05 level.
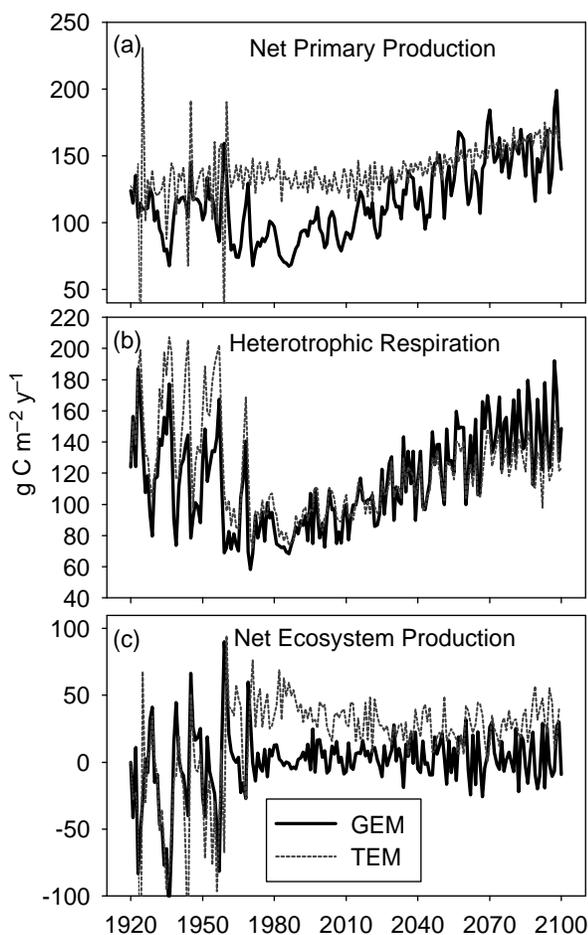
Fig. 6 Historical and projected interannual variation in (a) net primary production (NPP), (b) heterotrophic respiration (R_H) and (c) net ecosystem production (NEP) in the Toolik Lake grid cell from the simulations by GEM and TEM.

is different from the historical period for which there was no sensitivity. For the projected period, NPP and NMIN simulated by each model are more strongly correlated than in the historical period (Table 2).

Heterotrophic respiration. Both models estimate that R_H increases over the course of the projected period (Fig. 6b). As in the historical period, R_H in the projected period is coupled to soil moisture in both models (Table 2); R_H estimated by TEM appears to be more sensitive to soil moisture than R_H estimated by GEM (Table 2). In contrast to the results for the historical period, R_H in the projected period estimated by both models is sensitive to air temperature (Table 2), with GEM being more sensitive than TEM. As in the historical period, NMIN in GEM is tightly coupled to R_H in the projected period. Unlike the results for the historical period, the TEM estimates of NMIN are also correlated to R_H in the projected period (Table 2). Because NPP in both models depends substantially on NMIN, the coupling between NMIN and R_H in the projected period explains similarities in the temporal pattern of NPP simulated by the models. Although estimates of R_H for the projected period are highly correlated between the two models ($r^2 = 0.88$) and are similar at the beginning of the period (GEM, $107\,\mathrm{g\,C\,m^{-2}}$ per year; TEM, $97\,\mathrm{g\,C\,m^{-2}}$ per year), by the end of the period R_H estimated by GEM is higher (approximately $150\,\mathrm{g\,C\,m^{-2}}$ per year) than R_H estimated by TEM (approximately $123\,\mathrm{g\,C\,m^{-2}}$ per year).

Net ecosystem production. For the projected period, GEM estimates that annual NEP ranges from –26 to $32\,\mathrm{g\,C\,m^{-2}}$ per year, and that C storage increases $4.3\,\mathrm{g\,C\,m^{-2}}$ per year across the projected period (Fig. 6c). There is little change in C storage across the period because changes in R_H kept pace with changes in NPP. Although the difference between maximum and minimum annual NEP estimates for the projected period is similar between the models, minimum and maximum annual NEP estimated by TEM (0 and $57\,\mathrm{g\,C\,m^{-2}}$ per year) are higher than those estimated by GEM. The TEM simulation indicates that C storage increases $28\,\mathrm{g\,C\,m^{-2}}$ per year across the projected period because NPP remains approximately $28\,\mathrm{g\,C\,m^{-2}}$ per year higher than R_H throughout the
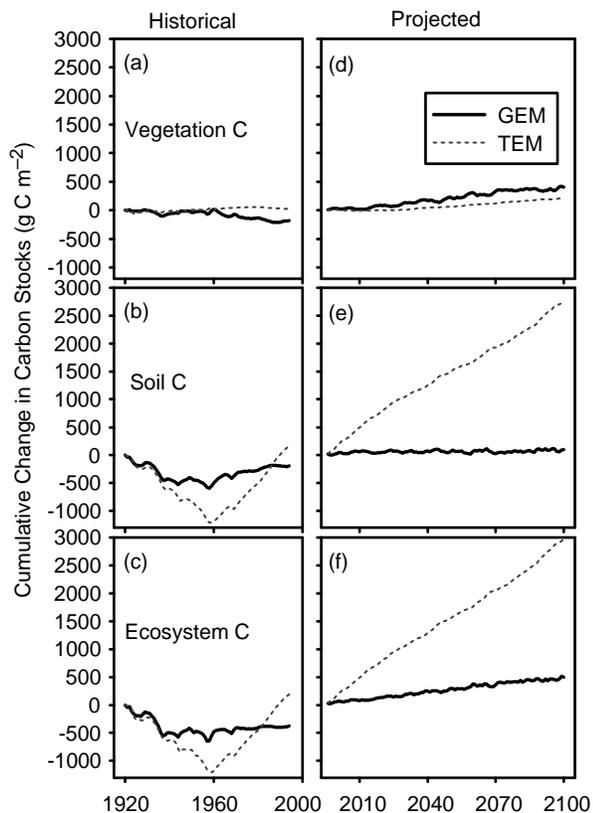
Fig. 7 Historical and projected changes in (a, d) vegetation C, (b, e) soil C and (c, f) ecosystem C for the Toolik Lake grid cell from simulations by GEM and TEM. Changes in C stocks are expressed as the change in $g\,m^{-2}$ since 1920 for the historical period and since 1995 for the projected period.

projected period. These different responses between GEM and TEM have important implications for C storage in the projected period.

Cumulative change in carbon storage. Both models estimate increases in vegetation C during the projected period, with GEM estimating a slightly larger increase than TEM (Fig. 7d). In the GEM simulation, the C:N ratio of vegetation increases from approximately 54 in 1995 to approximately 70 in 2100. Similarly, the C:N ratio of vegetation in the TEM simulation increases from approximately 47 in 1995 to 55 in 2100. During the projected period GEM estimates minimal changes in soil C (Fig. 7e). In contrast, TEM estimates a large increase in cumulative soil C storage over the projected period (Fig. 7e). Although the C:N ratio of vegetation increases during the projected period in the GEM simulations, the overall C:N ratio of soil organic matter remains stable at approximately 19.5 throughout both the historical and projected periods. In the TEM simulations, the increase in the C:N ratio of vegetation and the accumulation of soil C causes the ratio of C:N in soil organic matter to

increase from approximately 16.7 in 1995 to approximately 20.8 in 2100. The pattern of cumulative change in ecosystem C storage simulated by GEM is similar to the pattern of cumulative change in vegetation C because the soil C storage was minimal. In contrast, the pattern of cumulative change in ecosystem C simulated by TEM is similar to the pattern of cumulative change in soil C, because the change in vegetation C was minimal (Fig. 7f).

Sensitivity of TEM to parameterization of soil C:N dynamics

We hypothesized that the long-term dynamics of C storage simulated by GEM are driven by increases in R_H that track increases in NPP, because most of the additional C that enters the soil returns to the atmosphere through decomposition in the two fast C pools in the soil (i.e. acid soluble and extractives; see Fig. 1). To test the sensitivity of TEM to changes in soil C:N dynamics, we reparameterized TEM using the values of C and N for the fast pools in the GEM calibration ($1356\,g\,C\,m^{-2}$ and $27.1\,g\,N\,m^{-2}$). This reparameterization changes the soil C:N ratio from 16.36 to 50.24. The TEM simulation with the parameterization for fast soil C estimates cumulative changes in C stocks that are similar to those of GEM (Fig. 8a, c, d, f). Similar to the GEM simulation for the historical period, TEM simulates a slight decrease in vegetation C and an increase in soil C. During the projected period, the trends of change in soil C and ecosystem C are similar between GEM and TEM.

We used TEM to simulate C storage across moist tundra ecosystems north of 50°N between 1921 and 2100 with each of the parameterizations (reference and fast soil C). In comparison to the reference simulation, the simulation with the parameterization for fast soil C simulates less C storage in the projected period (Fig. 9, Fig. 10). The reference parameterization of TEM estimates cumulative C storage of $2032\,g\,C\,m^{-2}$ between 1995 and 2100 for moist tundra north of 50°N, which is substantially higher than the cumulative C storage of $463\,g\,C\,m^{-2}$ estimated by the parameterization for fast soil C dynamics. There are greater differences in simulated C storage across the pan-Arctic between the two parameterizations for the decade from 2085 to 2094 during the projected period than for the decade from 1985 to 1994 during the historical period (Fig. 10). Both simulations also show substantial spatial variability in C storage during both of these decades (Fig. 10).
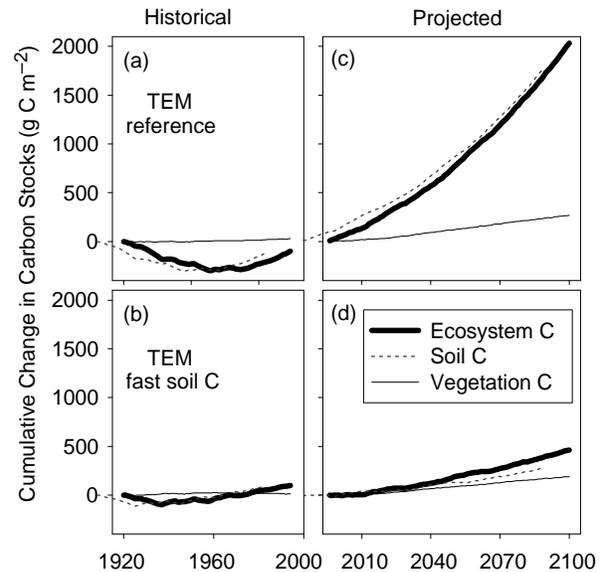
Discussion

The ability of different models to reproduce short-term responses of experiments is no guarantee that the models will have the same long-term responses (Rastetter 1996).
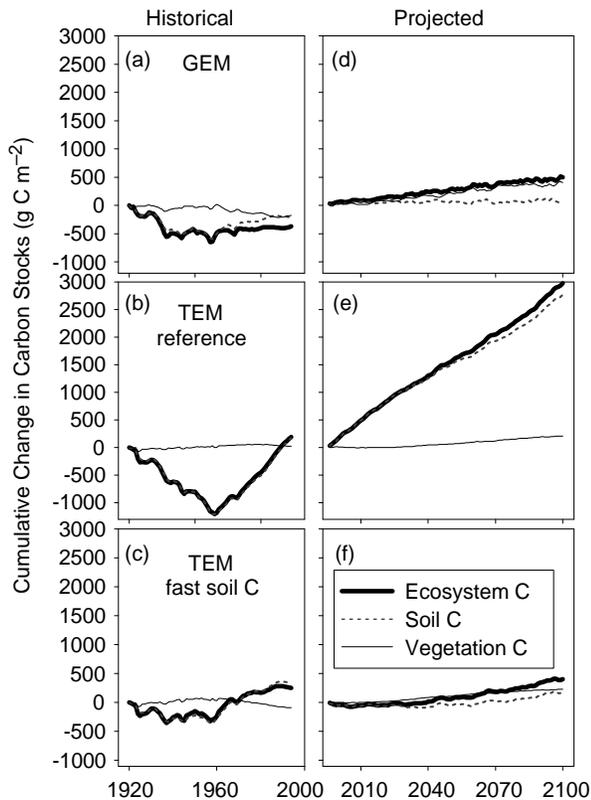
Fig. 8 Historical and projected changes in C stocks for the Toolik Lake grid cell simulated by (a) GEM, (b) TEM with the reference parameterization and (c) TEM with the parameterization for fast soil C dynamics. Changes in C stocks are expressed as the change in g m^{-2} since 1920 for the historical period and since 1995 for the projected period.

Fig. 9 Historical and projected changes in C stocks for moist tundra ecosystems north of 50°N simulated by (a) TEM with the reference parameterization and (b) TEM with the parameterization for fast soil C dynamics. Changes in C stocks are expressed as the change in g m^{-2} since 1920 for the historical period and since 1995 for the projected period.
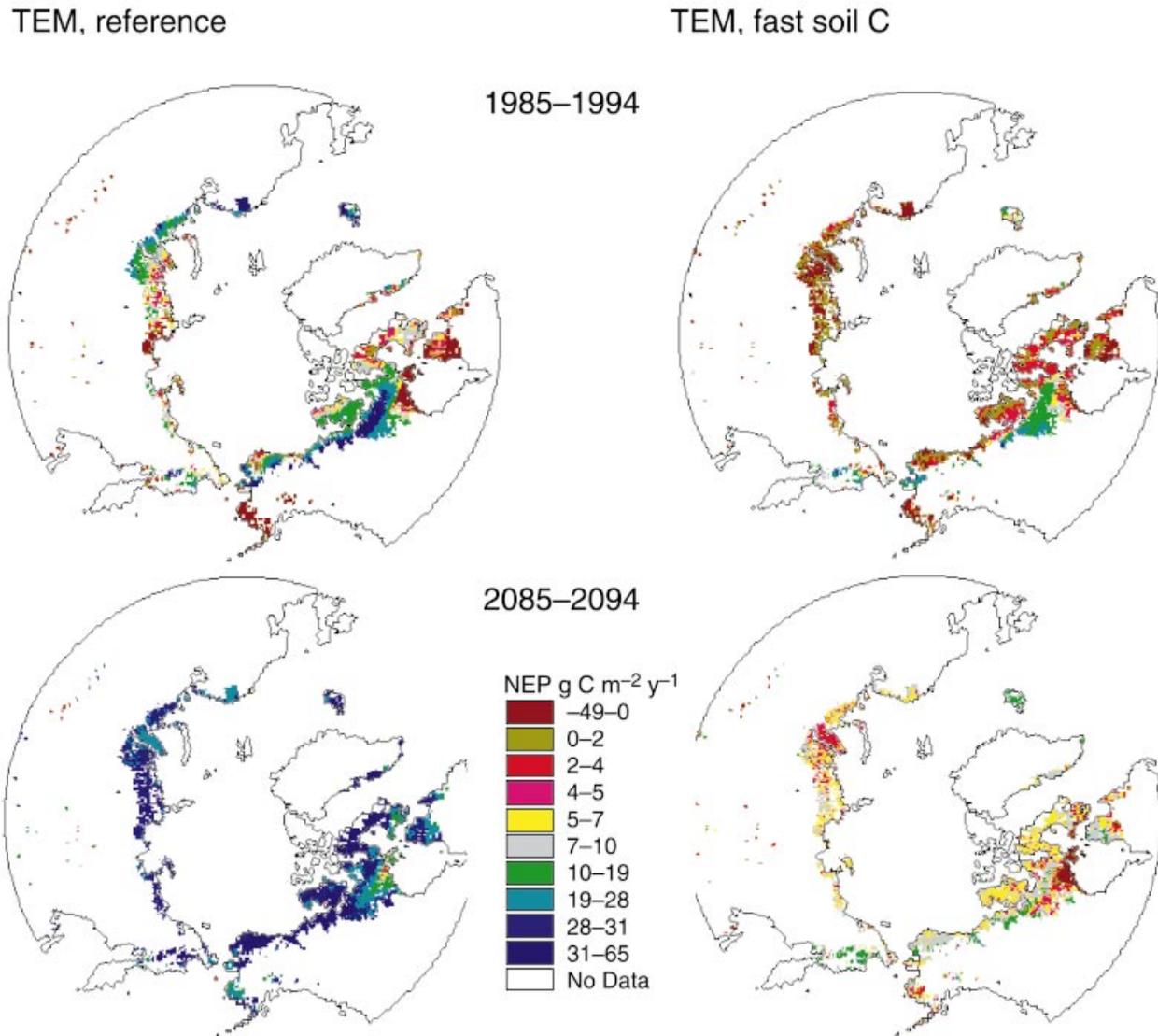
In this study, GEM and TEM both quantitatively reproduced the results from a 9-year experimental study (Chapin *et al.* 1995) and demonstrated acclimation responses similar to those observed in experiments that studied responses to step changes in atmospheric CO_2 (Oechel *et al.* 1992). Although dynamics in the historical period revealed different interannual sensitivities of NPP in the models, the long-term changes in C storage during the historical period were primarily driven by changes in soil C associated with the dynamics of R_H, which were similar between the two models. In contrast, the responses of C storage diverged in the projected period. This has been observed in other model comparisons in which models present rather consistent simulations of current conditions, but responses diverge substantially when climate and CO_2 are altered (VEMAP Members 1995; Pan *et al.* 1998; Kicklighter *et al.* 1999). In the GEM simulation during the projected period, increases in R_H track increases in NPP, whereas in the TEM simulation increases in R_H lag increases in NPP. In the projected period R_H simulated by GEM was more sensitive to air

temperature than R_H simulated by TEM. We inferred that the difference between the long-term C dynamics of the two models represent differences in the role of recalcitrant soil C in ecosystem C dynamics. By parameterizing TEM for the fast soil C pools in GEM, we demonstrated that the long-term response of the models to projected climate change appears to be related to the differences in how the models represent the role of recalcitrant soil C in long-term ecosystem C dynamics.

The difference in R_H response in the projected period is associated with differences in how N concentration of litter influences decomposition dynamics in the projected period. In the GEM simulation, the increase in the C:N ratio in vegetation is associated with the simulation of increased woodiness in tundra as climate warms (McKane *et al.* 1997a) and changes in vegetation N concentration associated with changes in C–N status of the vegetation as atmospheric CO_2 increases (Rastetter *et al.* 1991). Increased woodiness in response to warming of air temperature has been observed by Chapin *et al.* (1995) and Hobbie & Chapin (1998). In GEM, plant litter enters the soil as extractives, acid soluble, and acid insoluble fractions, which can later be converted into humus through a series of transformations (Fig. 1). The C:N ratios of these soil organic matter pools are assumed to be constant except for that of the extractives, which varies in response to the N concentration of litter. Changes in the bulk C:N ratio of soils in this model

TEM, reference

TEM, fast soil C

1985–1994

2085–2094

NEP g C m^{-2} y^{-1}

- -49–0
- 0–2
- 2–4
- 4–5
- 5–7
- 7–10
- 10–19
- 19–28
- 28–31
- 31–65
- No Data

Fig. 10 Simulated spatial and temporal variability in mean annual NEP in moist tundra ecosystems north of 50°N by TEM with the reference parameterization and by TEM with the parameterization for fast soil C dynamics for the decade from 1985 to 1994 and for the decade from 2085 to 2094.

result predominantly from a shift in the relative abundance of these four soil pools and, to a lesser extent, from changes in the C:N ratio of extractives. Changes in the relative abundance of the four soil pools in turn results from changes in the C:N ratio of litter, which determines the initial allocation of litter among extractives, acid soluble, and acid insoluble fractions, and on the availability of inorganic N, which limits transformations among the organic matter pools that require a net immobilization of N. Because humus dominates soil organic matter in this application of GEM and because humus has both a constant C:N ratio and a slow turnover time, it is difficult for changes in litter N concentration to substantially change the C:N ratio of bulk soil within the

200-year simulations. Thus, R_{H} is determined predominantly from the dynamics of the extractive and acid soluble pools, which turnover more rapidly.

In the TEM simulations, the vegetation N concentration is prescribed to decrease in a linear fashion with rising atmospheric CO_2 so that there is a 15% decrease for a 340 ppmv increase of atmospheric CO_2. This magnitude of change is the average change in vegetation N concentration observed over many studies (McGuire *et al.* 1995b), and the effects on decomposition are similar to those documented in McGuire *et al.* (1997). The representation of soil organic matter in TEM includes the simultaneous C and N dynamics of both decomposing litter and more

recalcitrant pools that are considered to be reactive in the context of climate change that might occur in the next century or so (McGuire *et al.* 1995a, 1997), i.e. reactive soil organic matter. The dynamics associated with the recalcitrant pool are effectively implemented with a target C:N ratio toward which the C:N ratio of soil organic matter tends over many years of decomposition. This target C:N is much lower than the C:N ratio of the incoming litter. An implicit assumption in TEM is that increases in the C:N ratio of inputs into the soil will cause the C:N ratio of reactive soil organic matter to increase, as was observed during the projected period in the TEM simulation for the reference parameterization. The shift in the soil C:N ratio represents the build-up of recalcitrant soil organic C during the projected period for the reference parameterization. In contrast, the parameterization for fast soil C effectively eliminated recalcitrant soil C from the dynamics by replacing the total soil C pool with a single, small, highly labile pool of soil C.

We have demonstrated that the differences in the long term soil C dynamics of GEM and TEM are related to interactions between parameterization model structure. These differences represent our incomplete understanding of how climate controls the dynamics of labile and recalcitrant soil C. Studies that have examined the isotopic signatures of C in soil organic matter have helped to elucidate the role of recalcitrant soil organic matter along environmental gradients in the tropical and the temperate zones (Trumbore 1993; Townsend *et al.* 1995). To our knowledge, experimental studies in tundra have not yet refined our understanding of soil processes to help us in reducing the uncertainty concerning the role of recalcitrant soil organic C in long-term ecosystem C dynamics. To date, much of the experimental effort on soil processes in tundra has focused on short-term controls over the release of C from soil (Oechel *et al.* 1995; Christensen *et al.* 1998; Moorhead *et al.* 1999) and nutrient availability to plants (Kielland & Chapin 1992; Nadelhoffer *et al.* 1992, 1997; Schimel *et al.* 1996). Studies have not yet been conducted to provide insight on C and N transformations that influence the long-term dynamics of soil C in Arctic tundra. Thus, the uncertainty we identified in this study represents our incomplete understanding of controls over C and N transformations in the long term dynamics of Arctic soils. Mechanistic studies on Arctic soils that improve understanding of the interaction among environmental factors, plant litter quantity and quality, and C and N transformations in controlling the long-term dynamics of Arctic soils are needed to reduce uncertainties and improve our ability to model the responses of Arctic ecosystems to global change.

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