Modelling carbon responses of tundra ecosystems to historical and projected climate: sensitivity of pan-Arctic carbon storage to temporal and spatial variation in climate

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Abstract

Historical and projected climate trends for high latitudes show substantial temporal and spatial variability. To identify uncertainties in simulating carbon (C) dynamics for pan-Arctic tundra, we compare the historical and projected responses of tundra C storage from 1921 to 2100 between simulations by the Terrestrial Ecosystem Model (TEM) for the pan-Arctic and the Kuparuk River Basin, which was the focus of an integrated study of C dynamics from 1994 to 1996. In the historical period from 1921 to 1994, the responses of net primary production (NPP) and heterotrophic respiration (R_H) simulated for the Kuparuk River Basin and the pan-Arctic are correlated with the same factors; NPP is positively correlated with net nitrogen mineralization (NMIN) and R_H is negatively correlated with mean annual soil moisture. In comparison to the historical period, the spatially aggregated responses of NPP and R_H for the Kuparuk River Basin and the pan-Arctic in our simulations for the projected period have different sensitivities to temperature, soil moisture and NMIN. In addition to being sensitive to soil moisture during the projected period, R_H is also sensitive to temperature and there is a significant correlation between R_H and NMIN. We interpret the increases in NPP during the projected period as being driven primarily by increases in NMIN, and that the correlation between NPP and temperature in the projected period is a result primarily of the causal linkage between temperature, R_H, and NMIN. Although similar factors appear to be controlling simulated regional-and biome-scale C dynamics, simulated C dynamics at the two scales differ in magnitude with higher increases in C storage simulated for the Kuparuk River Basin than for the pan-Arctic at the end of the historical period and throughout the projected period. Also, the results of the simulations indicate that responses of C storage show different climate sensitivities at regional and pan-Arctic spatial scales and that these sensitivities change across the temporal scope of the simulations. The results of the TEM simulations indicate that the scaling of C dynamics to a region of arctic tundra may not represent C dynamics of pan-Arctic tundra because of the limited spatial variation in climate and vegetation within a region relative to the pan-Arctic. For reducing uncertainties, our analyses highlight the importance of incorporating the understanding gained from process-level studies of C dynamics in a region of arctic tundra into process-based models that simulate C dynamics in a spatially explicit fashion across the spatial domain of pan-Arctic tundra. Also, efforts to improve gridded datasets of

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historical climate for the pan-Arctic would advance the ability to assess the responses of C dynamics for pan-Arctic tundra in a more realistic fashion. A major challenge will be to incorporate topographic controls over soil moisture in assessing the response of C storage for pan-Arctic tundra.

Keywords: carbon storage, climate change, net ecosystem production, pan-Arctic, Terrestrial Ecosystem Model, tundra ecosystems

Introduction

Surface air temperature has been increasing in many Arctic regions in recent decades (Beltrami & Mareschal 1991; Chapman & Walsh 1993; Everett & Fitzharris 1998; Sereeze et al. 1999). Since about 1970, mean annual temperature has been increasing markedly over both the Eurasian and north-west North American land masses. Trends locally exceed 0.5° per decade and are much larger than for the Northern Hemisphere as a whole, although there is also pronounced cooling over the western subpolar north Atlantic. Thus, some high-latitude regions are warming, other regions are cooling, and there is substantial interannual variability in climate across high latitudes (Everett & Fitzharris 1998). Thus, climatic trends at high latitudes are expected to exhibit substantial temporal and spatial heterogeneity.

Climate change at high latitudes has the potential to substantially influence the carbon (C) storage capacity of Arctic tundra (McGuire & Hobbie 1997), which contains 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). Efforts are underway to measure changes in C storage at one or several sites in different terrestrial ecosystems. For some of these efforts, the measurements have been extrapolated to continental-scale regions to identify the potential implications of the studies for terrestrial C storage (Fan et al. 1990; Oechel et al. 1993, 1997; Wofsy et al. 1993; Grace et al. 1995; Goulden et al. 1996). Extrapolations of this sort, which rely on an implicit assumption that measured changes in site-specific C storage are typical of a broader region or biome, are unable to account for spatial heterogeneity in climate and associated spatial heterogeneity in C exchange between terrestrial ecosystems and the atmosphere. In contrast, spatially explicit models of ecosystem processes are a tool that can be used to investigate the implications of spatial heterogeneity in climate for C storage of terrestrial ecosystems.

For example, the simulation of terrestrial C storage by the Terrestrial Ecosystem Model (TEM) in the Amazon Basin (Tian et al. 1998), which agrees with measurements of C storage made by three studies in the Amazon Basin (Fan et al. 1990; Grace et al. 1995; Miranda et al. 1997), indicates that measured changes in site-specific C storage may not be typical of a broader region because of spatial variability in climate across the region. The simulation by Tian et al. (1998) also indicates substantial interannual variability in C exchange between Amazonian ecosystems and the atmosphere, driven primarily by interannual variability in climate associated with El Niño cycles. Thus, annual estimates of C storage responses for large regions should be evaluated with a methodology that is temporally and spatially explicit.

In global applications of TEM, the parameterizations for tundra have been calibrated to the fluxes and pools measured at the Toolik Lake study site in Alaska (McGuire et al. 1992), a site which occurs within the Kuparuk River Basin. The Kuparuk River Basin, which is a region that has experienced warming in recent decades, has been the focus of the Arctic System Science Land–Atmosphere–Ice Interactions (ARCSS-LLAI) Flux Study (Weller et al. 1995; Kane & Reeburgh 1998), which evaluated C dynamics in the basin from 1994 to 1996 (Oechel et al. 1998; Fahnestock et al. 1998; Hobbie et al. 1998; Jones et al. 1998; Oberbauer et al. 1998; Walker et al. 1998). Although the ARCSS-LLAI Flux Study represents an important attempt to estimate regional C storage of tundra ecosystems, it is not clear if estimates of C storage from 1994 to 1996 of the Kuparuk River Basin are representative of pan-Arctic tundra. In this study we apply TEM to evaluate the potential sensitivity of simulated C storage for pan-Arctic tundra to temporal and spatial variation in climate by comparing responses of the model for pan-Arctic tundra to responses simulated for the Kuparuk River Basin.

Methods

Overview

In this study we apply TEM to simulate historical and projected C dynamics of the pan-Arctic between 1921 and 2100 for tundra ecosystems north of 50°N latitude at 0.5° resolution (latitude by longitude). For application to pan-Arctic tundra, TEM simulates the C dynamics of two vegetation types, one which includes polar desert and alpine tundra and the other which includes moist tundra
(Fig. 1). The cartographic sources of these vegetation types are documented in Melillo et al. (1993). The polar desert/alpine tundra of the TEM vegetation classification approximately corresponds to graminoid tundra in the circumpolar classification of Walker (2000), and the moist tundra of TEM approximately corresponds to dwarf-shrub graminoid tundra, low shrub tundra, and tall shrub tundra in the circumpolar classification. In this study we do not evaluate the transition zone between tundra and boreal forest, which is classified as boreal woodland in Fig. 1. We first evaluate the temporal variability of tundra C dynamics by comparing dynamics aggregated for pan-Arctic tundra to dynamics aggregated for the Kuparuk Basin. We analyse temporal variability in C dynamics separately for the historical and projected periods, and evaluate sensitivity of dynamics to some important issues concerning the nitrogen (N) cycle. Our analysis then evaluates spatial variability of tundra C dynamics by comparing the spatial variation in C dynamics across the pan-Arctic to spatial variation across the Kuparuk Basin for four different decades separated by 50-year intervals.

The Terrestrial Ecosystem Model (TEM)

The TEM is a process-based, global-scale ecosystem model that uses spatially referenced information on climate, elevation, soils, and vegetation to make monthly estimates of important C and N fluxes and pool sizes of the terrestrial biosphere (Fig. 2). Our application of TEM in this study is based on version 4.1 of the model (McGuire et al. 1997; Melillo et al. 1996a; McGuire et al. 1999) and preliminary analyses of this study, in which we modified version 4.1 of TEM specifically for application to tundra ecosystems. The modifications implemented in TEM include: (i) changing the formulation of decomposition so that temperature is maintained at 0°C when modelled snowpack is present (McGuire et al. 1999); (ii) increasing soil moisture by 30% water-filled pore space (WFPS) so that modelled WFPS matches observations of WFPS at several study sites in the Kuparuk Basin; (iii) changing the moisture response function of decomposition so that decomposition simulated by TEM has the same sensitivity to soil moisture as in McKane et al. (1997a); and (iv) implementing a nitrogen loss formulation that depends linearly on simulated available soil inorganic N.

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 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 pan-Arctic tundra ecosystems in this study, we calibrated TEM for polar desert/alpine tundra and for moist tundra to fluxes and pools measured at the Toolik Lake study site in Alaska (see table A1 in McGuire et al. 1992). The parameter that controls nitrogen losses from the model was calibrated so that simulated losses at equilibrium are 0.06 g N m⁻² y⁻¹ in response to nitrogen inputs of the same level; this level of N input is equivalent to N inputs measured at Toolik Lake (McKane et al. 1997b). Based on the review of McGuire et al. (1995b), we set the value of the parameter that defines how N concentration of vegetation changes with changes in atmospheric CO₂ so that vegetation N concentration decreases linearly by 15% for a 340 ppmv increase in CO₂ concentration (see McGuire et al. 1997). The fluxes and pools at the calibration site and other assumptions in parameterizing the model for polar desert/alpine tundra and for moist tundra are based primarily on Chapin et al. (1980), Shaver & Chapin (1986, 1991), Shaver et al. (1990), and Giblin et al. (1991). For the input variables associated with the Toolik Lake study site, simulations with TEM reproduce the fluxes and pools used to parameterize the model.

Input datasets and simulation protocol

Overview of input datasets. To examine spatial variability in C responses to climate change, we represented pan-Arctic tundra north of 50°N at 0.5° resolution (latitude × longitude) with 2566 grid cells classified as polar desert/alpine tundra and 3925 grid cells classified as moist tundra (Fig. 1). We simulated C dynamics of the pan-Arctic from 1921 to 2100, with the historical period spanning 1921–94 and the projected period spanning 1995–2100. The simulation of C dynamics of the pan-Arctic from 1921 to 2100 required that we organize a number of input datasets (Table 1). In any particular year, N inputs and atmospheric CO₂ are assumed to be constant across the pan-Arctic. Of these two variables, only atmospheric CO₂ varied temporally from 1921 to 2100. Other variables organized for these grid cells include vegetation, elevation, soil texture, cloudiness, air temperature, and precipitation. Of these variables, air temperature and precipitation had temporal variation from 1921 to 2100.

Nitrogen inputs and atmospheric CO₂. To simulate the influence of atmospheric N inputs, we annually added 0.06 g N m⁻² y⁻¹ to the inorganic N pool of TEM. This level of N input is equivalent to N inputs measured at Toolik Lake (McKane et al. 1997b). In this study, the historical CO₂ data were generated from ice core measurements and atmospheric CO₂ observations (Enting et al. 1994). The CO₂ concentrations increased

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Vegetation Types

- ice
- polar desert/alpine tundra
- moist tundra
- boreal woodlands
- boreal forest
- temperate forest
- temperate grassland

Fig. 1 Map of vegetation gridded at 0.5° resolution (latitude by longitude) north of 50°N. In this study, the Terrestrial Ecosystem Model (TEM) was used to simulate carbon dynamics for grid cells classified as polar desert/alpine tundra and as moist tundra.

Fig. 2 The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation ($C_V$); structural N in the vegetation ($N_{VS}$); labile N in the vegetation ($N_{VL}$); organic carbon in soils and detritus ($C_S$); organic N in soils and detritus ($N_S$); and available soil inorganic N ($N_{AV}$). Arrows show C and N fluxes; GPP, gross primary production; $R_A$, autotrophic respiration; $R_H$, heterotrophic respiration; $L_C$, litterfall carbon; $L_N$, litterfall N; NUPTAKE$_L$, N uptake into the structural N pool of the vegetation; NUPTAKE$_S$, 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 NLOSS, N losses from the ecosystem.

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Fig. 3 Mean annual air temperature as °C (a), annual precipitation as mm (b); and mean simulated annual soil moisture as percent water filled pore space, WFPS (c) of the pan-Arctic (solid line) and the Kuparuk Basin (dotted line) between 1921 and 2100. The shaded region represents the standard deviation across the pan-Arctic.

Fig. 4 Spatial distribution of mean annual temperature (MAT) as °C throughout the pan-Arctic during four decades separated by 50 years during the simulation period from 1921 to 2100: 1935–44 (a); 1985–94 (b); 2035–2044 (c); and 2085–2094 (d).

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from 302 ppmv in 1921 to 361 ppmv in 1994. The projected CO₂ data were derived from radiative forcing in the Hadley CM2 climate simulation, which is based on the heat-trapping potential equivalent to a 1% annual increase in atmospheric CO₂ (Mitchell et al. 1995). The radiative forcing depends on the heat-trapping potential of all radiatively active gases in the atmosphere. Because atmospheric CO₂ is estimated to be responsible for 63% of historical radiative forcing and is projected to be responsible for 76% to 84% of radiative forcing at the end of the next century (IPCC 1994, 1995), we assumed that atmospheric CO₂ accounts for 70% of the radiative forcing in the projected period of our simulations. Thus, from 1995 to 2100 we increased atmospheric CO₂ by 0.7% annually starting with 361 ppmv in 1994.

Elevation, soil texture, and cloudiness. Elevation affects snowmelt in TEM (Vörösmarty et al. 1989) and thereby influences soil moisture. The elevation data set used in this study represents an aggregation to the half-degree resolution of the NCAR/Navy global 10-minute elevation data set (NCAR/Navy 1984). Soil texture, which is used as percent silt plus clay by TEM, is based on the digitization of the FAO-UNESCO (1971) soil map (see Vörösmarty et al. 1989). Mean monthly cloudiness in this study is calculated as 100% minus percent monthly sunshine duration from the global datasets of Cramer & Leemans (Cramer, pers. comm.), which is a major update of the dataset described in Leemans & Cramer (1991). The Cramer & Leemans data set of percentage monthly sunshine duration was developed from weather station data on the fraction of cloud-free days during the month. These observations were interpolated to a global half-degree grid using a 3D smoothing spline function.

Temperature and precipitation. Historical temperature and precipitation anomalies from 1900 to 1994 were developed to half-degree spatial resolution for the globe at the Max-Planck Institute for Meteorology (Heimann, unpubl. data) by interpolating the temperature anomalies of Jones (1994) and the precipitation anomalies of Hulme (1995). We added the monthly temperature and precipitation anomalies for the period from 1921 to 1994 from this data set to the long-term monthly air temperatures and precipitation database of Legates & Willmott (1990a, 1990b) to create historical temperature and precipitation data from 1921 to 1994. Arctic precipitation estimates are known to contain large errors because of gauge undercatch of solid precipitation (Grossman et al. 1991). Although Legates & Willmott (1990b) made efforts to correct for the undercatch, there may be substantial interpolation bias associated with the sparse network of weather station across the pan-Arctic. While biases likely remain, the Legates and Willmott climatology for high latitudes represents the best available base climatology to which anomalies can be added.

Our datasets of air temperature and precipitation for the projected period 1995–2100, are based on monthly temperature and precipitation ramps defined from a transient climate simulation of the Hadley Center CM2 model, which considered the combined effect of radiative forcing associated with both changes in greenhouse gases and sulphate aerosols (Mitchell et al. 1995; IPCC 1996; WGI, Sections 5 and 6). These ramps are based on temperature differences or precipitation ratios between the 30-y period from 2070 to 2099 and the 30-y period from 1961 to 1990 in the Hadley CM2 simulation (see Neilson 1998). We used these temperature and precipitation differences to define monthly ramps of long-term changes in monthly temperature and precipitation between 1995 and 2100 for each grid cell classified as tundra north of 50°N. The monthly temperature and precipitation in 1995 was defined as the mean monthly temperature and precipitation for the years 1969 through 1994. We added interannual variability to each year on the ramp by: (i) randomly selecting a year between 1969 and 1994; (ii) calculating each monthly anomaly for temperature and precipitation from the long-term monthly means between 1969 and 1994 for the randomly selected year; and (iii) adding each monthly anomaly to the appropriate monthly temperature or precipitation value along the ramp.

Table 1 Input variables for TEM simulations. Description of spatial and temporal resolution and temporal scope of each variable
During the historical period, the temperature of the pan-Arctic varies within approximately two degrees of 
-8 °C until the 1970s (Fig. 3). After the 1970s, temperature of the pan-Arctic increases to approximately 
-5 °C. In comparison, the temperature of the Kuparuk remains approximately 2 °C less than temperature of the pan-
Arctic throughout the historical and projected periods. The spatial variability in mean annual temperature across the pan-Arctic has a standard deviation of approximately 10 °C until the 1970s, when it begins to 
gradually diminish to approximately 5 °C by the end of the projected period. For four decades that are separated 
by 50 years during the simulation period, temperature increases north to south as expected (Fig. 4). In the 
historical decades, the coldest regions are in the Canadian Archipelago north of Hudson Bay and in 
central Siberia, with warmer regions in eastern Siberia, Alaska, eastern Greenland, and northern Europe. For 
decades in the projected period, all regions become warmer, but central Siberia warms at a faster rate than the 
Canadian Archipelago.

At the beginning of the historical period, precipitation of the pan-Arctic varied between approximately 300 
mm y⁻¹ and 500 mm y⁻¹ until the 1960s at which time it increases gradually to approximately 900 mm y⁻¹ by the 
end of the historical period (Fig. 3). In contrast, precipitation of the Kuparuk Basin varied between 100 mm y⁻¹ 
and 400 mm y⁻¹ until 1969, at which time it increased abruptly to approximately 1000 mm y⁻¹ for the remain-
der of the historical period. Throughout the projected period, precipitation of the pan-Arctic varied between 
approximately 600 mm y⁻¹ and 1200 mm y⁻¹, which is similar to the temporal pattern for the Kuparuk Basin. 
The spatial variability in precipitation across the pan-Arctic has a standard deviation of approximately 200 mm y⁻¹ 
at the start of the historical period, but increases to 500 mm y⁻¹ by the end of the historical period and remains at 500 mm y⁻¹ throughout the projected period. Similar to the temporal trend for precipitation of the whole pan-Arctic, precipitation across the pan-Arctic increases between an early decade of the historical period and a later decade of the historical period, and remains essentially unchanged during the decades we examined in the projected period (Fig. 5).

**Simulation protocol.** To initialize the simulation, we ran TEM to equilibrium for each of the tundra grid cells of the pan-Arctic, i.e. tundra grid cells north of 50°N, using an average climate between 1921 and 1930. For each grid 
cell, average climate between 1921 and 1930 was calculated for each month of the year as the mean monthly temperature and precipitation from 1921 through 1930. The equilibrium pools of C and N estimated for this climate were used as the initial conditions for simulating the temporal dynamics of C storage from 1921 to 2100.

**Results**

**Temporal and spatial variation in simulated soil moisture**

During the historical period, simulated soil moisture of the pan-Arctic generally oscillated between 80% and 85% 
water-filled pore space (WFPS: Fig. 3). In contrast, simulated soil moisture of the Kuparuk Basin generally 
oscillated between 70% and 85% WFPS until around 1969 when it became fairly stable between 85% and 90% WFPS 
through the remainder of the historical period. Simulated soil moisture decreased slightly in the projected period, 
but tended to remain between 80% and 85% WFPS in the pan-Arctic and between 85% and 90% WFPS in the 
Kuparuk Basin. Spatial variability of simulated soil moisture across the pan-Arctic had a standard deviation of 
10% throughout the historical and projected periods. Similar to precipitation, simulated soil moisture increase 
throughout the pan-Arctic between early and late decades of the historical period (Fig. 6). In general, the spatial pattern of soil moisture in the decades we examined in the projected period is similar to the spatial pattern in the last decade of the historical period.

**Temporal responses of NPP, R_H, and NEP to historical climate**

Simulated annual NPP for the pan-Arctic increases from 83 g C m⁻² y⁻¹ in 1921 to 88 g C m⁻² y⁻¹ in 1994. Between 
95% and 100% of annual NPP occurs during June, July, 
and August. In any particular year, NPP is within approximately 7 g C m⁻² y⁻¹ above and below the 
temporal trend (Fig. 7a). The estimates of annual NPP for the pan-Arctic are generally lower than annual NPP for the 
Kuparuk Basin, and demonstrate considerably less interannual variation during the historical period. 
Estimates of annual NPP for the pan-Arctic and Kuparuk Basin are not correlated with temperature or 
simulated soil moisture, but are correlated with simulated annual NMIN (Table 2). Although simulated annual NPP for both the pan-Arctic and Kuparuk tends to increase with increases in annual NMIN, the strength of the association is stronger for the pan-Arctic (Fig. 8a).

Simulated annual R_H of the pan-Arctic has a peak to trough oscillation of approximately 20 g C m⁻² y⁻¹ with 
a period of about 10 years until the 1970s, after which the interannual variability in R_H decreases substantially 
(Fig. 7b). Between the beginning and end of the historical period, annual R_H of the pan-Arctic decreases from 83 to 
79 g C m⁻² y⁻¹. In any particular year, between 35% and
Fig. 5 Spatial distribution of annual precipitation (AP) as mm throughout the pan-Arctic during four decades separated by 50 years during the simulation period from 1921 to 2100: 1935–44 (a); 1985–94 (b); 2035–2044 (c); and 2085–2094 (d).

40% of annual $R_H$ occurs in June, July, and August. Although the trend in simulated annual $R_H$ for the pan-Arctic is similar to the trend for the Kuparuk Basin between the beginning and end of the historical period, the interannual variability of pan-Arctic $R_H$ is much smaller than Kuparuk $R_H$. For both the pan-Arctic and the Kuparuk Basin, simulated $R_H$ is tightly coupled to soil moisture, but is not correlated with either temperature or NMIN (Table 2), which indicates that $R_H$ increases as soils dry in arctic tundra (Fig. 8b).

At the beginning of the historical period, simulated pan-Arctic NPP, which is the difference between pan-Arctic NPP and $R_H$, is 0 g C m$^{-2}$ y$^{-1}$, indicating that TEM is in equilibrium prior to simulating historical C dynamics. For the historical period, TEM estimates that annual NPP of the pan-Arctic varies between -18 and 16 g C m$^{-2}$ y$^{-1}$ and that mean C storage of pan-Arctic tundra decreases slightly by 1 g C m$^{-2}$ y$^{-1}$ (Fig. 7c).

Between the beginning of the historical period and approximately 1970, the temporal pattern of simulated annual NEP for the pan-Arctic is similar to the pattern for the Kuparuk, but the magnitude of variability is much less for the pan-Arctic simulation. During this period the temporal variation in simulated annual NEP for the pan-Arctic tends to track the temporal variation in $R_H$ ($r^2 = 0.77$). For the final 25 years of the historical period, simulated annual NEP of the pan-Arctic is approximately 10 g C m$^{-2}$ y$^{-1}$, which is substantially less than the estimate for the Kuparuk, which fluctuates around 25 g C m$^{-2}$ y$^{-1}$.

**Temporal responses of NPP, $R_H$, and NEP to projected climate**

Simulated annual NPP for the pan-Arctic increases from 91 g C m$^{-2}$ y$^{-1}$ in 1995 to 129 g C m$^{-2}$ y$^{-1}$ in 2100.
historical period, the proportion of $R_{H}$ in June, July, and August increases from between 35% and 40% to between 40% and 45% in the projected period, which indicates that decomposition during these summer months increases at a greater rate relative to other months of the year. Although the trend in simulated annual $R_{H}$ for the pan-Arctic is similar to the trend for the Kuparuk Basin between the beginning and end of the projected period, the interannual variability of pan-Arctic $R_{H}$ is smaller than Kuparuk $R_{H}$. In contrast to the historical period, simulated annual $R_{H}$ is correlated with temperature for both the pan-Arctic and the Kuparuk (Table 2). Although the relationship between simulated annual $R_{H}$ and soil moisture for both the pan-Arctic and the Kuparuk Basin indicate that $R_{H}$ is more sensitive to changes in soil moisture in the projected period than in the historical period (Fig. 8d), the strength of the correlations is weaker in the projected period (Table 2). The correlation for the pan-Arctic in the projected period is weaker than the correlation for the Kuparuk Basin (Table 2). In contrast to the historical period, simulated annual $R_{H}$ and annual NMIN are correlated for both the pan-Arctic and the Kuparuk Basin (Table 2).

For the projected period, TEM estimates that annual NPP of the pan-Arctic varies between -1 and 32 g C m$^{-2}$ y$^{-1}$, and that mean C storage of pan-Arctic tundra increases by 16 g C m$^{-2}$ y$^{-1}$ (Fig. 7c). Simulated annual NPP gradually increases from 12 g C m$^{-2}$ y$^{-1}$ at the beginning of the projected period to 22 g C m$^{-2}$ y$^{-1}$ by the end of the period because NPP is increasing more steeply than $R_{H}$ throughout the projected period. The gradual increase in simulated NPP of the pan-Arctic contrasts with the temporal dynamics of NPP simulated for the Kuparuk Basin in the projected period, where simulated NPP remains approximately 25 g C m$^{-2}$ y$^{-1}$ higher than $R_{H}$ throughout the projected period (Fig. 7c).

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**Table 2** Proportion of variation explained by correlation of simulated annual net primary production (NPP) and annual heterotrophic respiration ($R_{H}$) of the pan-Arctic and the Kuparuk River Basin during the historical and projected periods with other variables including mean annual temperature (MAT), mean annual soil moisture (MASM), and annual net nitrogen mineralization (NMIN). Proportion of variation explained by correlations of simulated annual NPP and $R_{H}$ with mean summer (June, July, and August) temperature and mean summer soil moisture is similar to the variation explained by correlations with MAT and MASM.

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$^1$ no correlation, as evaluated by significance at the 0.05 level.
Fig. 6 Spatial distribution of mean annual soil moisture as percent water filled pore space (%WFPS) throughout the pan-Arctic during four decades separated by 50 years during the simulation period from 1921 to 2100: 1935–44 (a) 1985–94 (b); 2035–2044 (c); and 2085–2094 (d).

Compared to the historical period, the proportion of annual NPP that occurs in June, July, and August drops from between 95% and 100% to between 90% and 95% in the projected period, which is indicative of a longer growing season. In any particular year, annual NPP is within approximately 10 g C m$^{-2}$ y$^{-1}$ above and below the temporal trend (Fig. 7a). Similar to the historical period, the estimates of annual NPP for the pan-Arctic in the projected period are generally lower than estimated annual NPP for the Kuparuk Basin. In contrast to the historical period, simulated annual NPP and temperature for the pan-Arctic are highly correlated in the projected period, and this correlation is substantially stronger than the correlation between simulated annual NPP and temperature of the Kuparuk Basin (Table 2). Similar to the historical period, simulated annual NPP and soil moisture for the pan-Arctic are uncorrelated, while simulated annual NPP and soil moisture for the Kuparuk Basin are weakly correlated. Similar to the historical period, the strength of the correlation between simulated annual NPP and NMIN for the pan-Arctic is higher than the correlation between simulated annual NPP and NMIN for the Kuparuk Basin (Table 2). In comparison to the historical period, estimates of annual NPP and NMIN for the pan-Arctic and the Kuparuk are more strongly correlated in the projected period (Table 2). In addition NPP is more sensitive to NMIN in the projected period than in the historical period (Fig. 8a, c).

Between the beginning and end of the projected period, simulated annual $R_{pp}$ of the pan-Arctic increases from 79 to 106 g C m$^{-2}$ y$^{-1}$, with an interannual variability that is within approximately 5 g C m$^{-2}$ y$^{-1}$ above and below the temporal trend (Fig. 7b). Compared to the
Fig. 8 The relationships between annual net primary production (NPP) as g C m⁻² y⁻¹ and annual net nitrogen mineralization (NMIN) as g N m⁻² y⁻¹ for the historical period (a); between annual heterotrophic respiration (RH) as g C m⁻² y⁻¹ and mean annual soil moisture (MASM) as percent water filled pore space during the historical period (b); between NPP and NMIN for the projected period (c); and between RH and MASM during the projected period (d). Annual estimates for tundra of the pan-Arctic (filled circles) and the Kuparuk River Basin (open circles) are shown with least-squares regression lines.

To assess the degree to which pan-Arctic responses during the projected period were driven by changes in atmospheric CO₂ vs. changes in climate, we conducted two additional simulations to estimate responses to changes in only atmospheric CO₂ and to changes in only climate. Across the projected period, the average long-term increase in NPP was similar between the two simulations, and each represented about half of the long-term NPP in the simulation that considered changes in both CO₂ and climate. The long-term response of RH was slightly negative for the simulation based on changes in only CO₂, whereas it was similar between the simulations based on climate change alone and the combination of changes in CO₂ and climate. Therefore, C storage simulated for the projected period was substantially higher for the simulation based on changes in only CO₂ in comparison to the simulation based on changes in only climate.

Because the response of C storage to elevated CO₂ in previous versions of TEM was quite sensitive to the value of parameter that defines how the N concentration of vegetation changes with changes in CO₂ concentration, we conducted a simulation driven by changes in both CO₂ and climate in which vegetation N concentration does not change as CO₂ increases. In this simulation, the response of C storage in the projected period was quite similar to the response we obtained from the previous simulation in which the model was driven by changes in only climate. Thus, the simulated response of pan-Arctic C storage to changes in climate and CO₂ depends substantially on assumptions about how vegetation N concentration changes in response to changes in atmospheric CO₂.

Spatial variability in responses of NPP, RH, and NEP to decadal patterns in climate

During the historical period, the spatial variability in simulated annual NPP and RH across the pan-Arctic has a standard deviation of approximately 40 g C m⁻² y⁻¹ (Fig. 7a, b). The standard deviation in simulated annual NPP and RH across the pan-Arctic increases from approximately 40 g C m⁻² y⁻¹ at the beginning of the projected period to approximately 50 g C m⁻² y⁻¹ by the end of the projected period (Fig. 7a, b). During both the historical and projected periods, the spatial variability in simulated annual NEP across the pan-Arctic has a standard deviation that is generally between 20 and 30 g C m⁻² y⁻¹ (Fig. 7c).

Although the gradual increase in simulated C storage for pan-Arctic tundra through the historical and projected periods can be observed in the decadal NEP.
patterns of four different decades separated by 50 years (Fig. 9), changes do not occur uniformly across all regions of the pan-Arctic. For example, compared to the NEP patterns for the decade between 1935 and 1944 (Fig. 9a), simulated mean annual NEP across the pan-Arctic between 1985 and 1994 (Fig. 9b) tended to increase up to 55 gC m$^{-2}$ y$^{-1}$ on much of the North American mainland, while C storage in north-central Asia still tends to increase up to 20 gC m$^{-2}$ y$^{-1}$. As another example, simulated NEP increases for the decade between 2035 and 2044 (Fig. 9c) are higher in some regions and lower in others in comparison to the NEP patterns for the decade between 1985 and 1994 (Fig. 9b).

To examine the issue of spatial sensitivity of C dynamics to climate at pan-Arctic and regional scales, we compared the proportion of variation in decadal patterns of NPP, $R_H$, and NEP explained by decadal patterns of temperature and soil moisture between the pan-Arctic and the Kuparuk Basin (Table 3). Across the pan-Arctic, spatial variation in NPP and $R_H$ is more correlated with decadal temperature than with decadal soil moisture during each of the decades we analysed, but the difference is reduced for the two projected decades (Table 3). A similar pattern is observed for the two vegetation types across the pan-Arctic, but the correlations with soil moisture are stronger in moist tundra than in polar desert/alpine tundra (Table 4). In contrast to the pan-Arctic, spatial variation across the Kuparuk Basin in simulated NPP and $R_H$ is strongly correlated with both temperature and soil moisture during all decades (Table 3). The correlations for the Kuparuk, which is composed of only moist tundra grid cells in our simulations, differ from the correlations for moist
Table 3 Proportion of variation explained by correlation of simulated annual net primary production (NPP), heterotrophic respiration (R_H), and net ecosystem production (NEP) of the pan-Arctic and the Kuparuk River Basin during different decades of the historical and projected periods with other variables including mean annual temperature (MAT) and mean annual soil moisture (MASM).

<table>
<thead>
<tr>
<th></th>
<th>Pan-Arctic (N = 5942 grid cells)</th>
<th>Kuparuk River Basin (N = 19 grid cells)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MAT</td>
<td>MASM</td>
</tr>
<tr>
<td>1935-44</td>
<td>NPP</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>0.18</td>
</tr>
<tr>
<td>1985-94</td>
<td>NPP</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>2035-2044</td>
<td>NPP</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>2085-2094</td>
<td>NPP</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>&lt;0.10</td>
</tr>
</tbody>
</table>

Table 4 Proportion of variation explained by correlation of simulated net primary production (NPP), heterotrophic respiration (R_H), and net ecosystem production (NEP) of pan-Arctic polar desert/alpine tundra and moist tundra during different decades of the historical and projected periods with other variables including mean annual temperature (MAT) and mean annual soil moisture (MASM).

<table>
<thead>
<tr>
<th></th>
<th>Polar desert/alpine tundra (N = 3614 grid cells)</th>
<th>Moist tundra (N = 2328 grid cells)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MAT</td>
<td>MASM</td>
</tr>
<tr>
<td>1935-44</td>
<td>NPP</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>0.17</td>
</tr>
<tr>
<td>1985-94</td>
<td>NPP</td>
<td>0.56</td>
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<tr>
<td></td>
<td>R_H</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>2035-2044</td>
<td>NPP</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>2085-2094</td>
<td>NPP</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>R_H</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>&lt;0.10</td>
</tr>
</tbody>
</table>

tundra across the pan-Arctic. The difference between regional and pan-Arctic sensitivities of C dynamics to temperature and soil moisture suggests that regional variability in climate is important in determining patterns of pan-Arctic C storage.

Simulated NEP across the pan-Arctic is weakly correlated with decadal temperature and soil moisture for all the decades we examined (Table 3). Across polar desert/alpine tundra, responses of C storage are also weakly correlated with decadal temperature and soil moisture in all four decades (Table 4). Simulated NEP in moist tundra is more correlated with soil moisture than with temperature, and in the decade between 1985 and 1994 the correlation is quite strong (Table 4). For the Kuparuk Basin, simulated decadal responses of C storage are strongly correlated with decadal temperature and soil moisture in the historical decades, uncorrelated in the decade between 2035 and 2044, and intermediate in the last decade that we examined during the projected period (Table 3). Our analyses indicate that the simulated decadal responses of C storage across the pan-Arctic were similarly correlated to decadal temperature and soil moisture between different decades of the projected period, and that the strength of the correlations is similar to the strength observed in the historical period. In contrast, the correlation of C storage to variation in temperature and soil moisture across the Kuparuk varies for different decades of the projected period, and the strength of the correlation is lower than in the historical period.

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Discussion

Recent annual temperature trends in the pan-Arctic are dominated by temperature changes during winter and to a lesser extent spring (Serreze et al. 1999). About half of the winter changes can be explained by interactions between the North Atlantic Oscillation (NAO) and the Southern Oscillation (Hurrell 1995, 1996). The NAO depends on the strengths of the Icelandic Low and the Azores High (Serreze et al. 1997), while the Southern Oscillation represents the atmospheric component of the El Niño Southern Oscillation (ENSO). About half of the observed warming in the pan-Arctic cannot be directly related to atmospheric circulation, and the pattern of warming is broadly consistent with model predictions of radiative forcing of the climate system associated with anthropogenic enhancement of greenhouse gases in the atmosphere (Serreze et al. 1999). Anthropogenic forcing is also suggested to be an important factor by palaeoclimate reconstructions, which indicate that the 20th Century is the warmest of the past 400 years (Overpeck et al. 1997). Furthermore, recent modelling studies suggest that anthropogenic forcing may modulate the intensity and frequency of variability such as the NAO and ENSO (Broccoli et al. 1998; Osborn et al. 1999). Thus, climatic change at high latitudes is expected to be characterized by substantial temporal and spatial variability. Because regional differences in climate trends have consequences for responses of C storage in the pan-Arctic, we compared the pan-Arctic responses of TEM to responses simulated for the Kuparuk River Basin, a region that has experienced warming in recent decades and has been the focus of a large integrated project to study the dynamics of C storage in arctic tundra between 1994 and 1996. In this discussion we first evaluate the degree to which the responses simulated for the Kuparuk River Basin represent the responses of pan-Arctic tundra. We then discuss uncertainties that limit the ability to assess regional and pan-Arctic responses of tundra C dynamics to historical and future climate change.

Carbon dynamics of the Kuparuk River Basin and the pan-Arctic

Our analysis indicates that the spatially aggregated responses of NPP and \( R_H \) for the Kuparuk River Basin and the pan-Arctic are correlated with the same factors in the historical period; i.e. NPP is positively correlated with NMIN and \( R_H \) is negatively correlated with soil moisture. The positive relationship between NPP and NMIN is consistent with the results of several experimental studies of fertilized plots (Shaver & Chapin 1980, 1986; Chapin et al. 1995). The negative relationship between \( R_H \) and soil moisture is consistent with plot-level studies that have documented higher soil C fluxes associated with a lower water table in arctic tundra (Oechel et al. 1993, 1995, 1997; Vourlitis & Oechel 1997, 1999; Christensen et al. 1998).

In comparison with the historical period, the spatially aggregated responses of NPP and \( R_H \) for the Kuparuk River Basin and the pan-Arctic in our simulations for the projected period have different sensitivities to temperature, soil moisture and NMIN. In addition to being sensitive to soil moisture, \( R_H \) is also sensitive to temperature and there is a significant correlation between \( R_H \) and NMIN. Because the gross N mineralization component of the NMIN formulation in TEM is tightly coupled to \( R_H \) (Raich et al. 1991), we interpret the association between \( R_H \) and NMIN as causal with increases in \( R_H \) driving increases in NMIN during the projected period. The increases in \( R_H \) are driven primarily by increases in temperature that tend to increase decomposition while soil moisture tends to remain fairly stable throughout the projected period for both the Kuparuk Basin and pan-Arctic. The increases in NPP throughout the projected period are associated with increases in temperature and NMIN for both the Kuparuk Basin and the pan-Arctic. Thus, we interpret the increases in NPP as being driven primarily by increases in NMIN, and that the correlation between NPP and temperature in the projected period is a result primarily of the causal linkage between temperature, \( R_H \), and NMIN.

It is possible that the NPP increases observed for the pan-Arctic during the projected period might be associated with N inputs from atmospheric deposition that could cause N to be accumulating in tundra ecosystems. To evaluate this issue we conducted two additional simulations. First, we conducted a simulation in which we closed the N cycle after initializing the model so that there were no N inputs or losses. Secondly, we conducted a simulation in which we allowed N inputs, but no N losses. The results of these additional simulations were virtually identical to the original simulation conducted for this study. It is important to recognize that the level of N inputs we used in our simulations is a background level of N deposition, and does not represent potential responses of ecosystem processes to anthropogenic N deposition associated with the burning of fossil fuels. Our simulations also do not consider N fixation, a process which may also respond to changes in climate and atmospheric CO\(_2\). With respect to the simulated increases in NPP during the projected period, we feel confident that the increases were driven primarily by the increases in NMIN, which were caused by increases in \( R_H \) associated with increases in temperature. Thus, we interpret the different correlations for simulated C dynamics between the historical and projected periods as the result
of non-linear interactions among C, N, and water
dynamics simulated by TEM.

Although similar factors appear to be controlling
simulated regional-and biome-scale C dynamics, simu-
lated C dynamics at the two scales differ in magnitude. At
the end of the historical period, increases in simulated C
storage are approximately two and one-half times greater
for the Kuparuk River Basin (approximately 25 g C m\(^{-2}\)
y\(^{-1}\)) than for pan-Arctic tundra (approximately 10 g C m\(^{-2}\)
y\(^{-1}\)). A recent IPCC analysis estimates that terrestrial sinks
besides Northern Hemisphere forest regrowth account for
\(1.3 \times 10^{15} \text{ g C y}^{-1}\) over the 1980s, and are associated
primarily with functional responses of terrestrial ecosys-
tems to \(\text{CO}_2\) fertilization, N deposition, and climatic
anomalies (Schimel \textit{et al.} 1996). The IPCC estimate
represents a functional sink strength of approximately
10 g C m\(^{-2}\) y\(^{-1}\) across the terrestrial biosphere, which
encompasses an area of approximately \(130 \times 10^{12} \text{ m}^2\)
(McGuire \textit{et al.} 1997). Thus, the TEM simulation for the
pan-Arctic estimates that increases in C storage for tundra
ecosystems in the 1980s are typical of the average sink
strength of the terrestrial biosphere associated with
functional responses. In contrast, if we assume the
estimate of increased C storage from the simulation for
the Kuparuk River Basin is typical of the pan-Arctic, then
we would conclude that the relative sink strength of
tundra is two and a half times greater than the average
functional sink strength of the terrestrial biosphere.
Similar to the end of the historical period, increases in
simulated C storage over the projected period are greater
for the Kuparuk River Basin (25 g C m\(^{-2}\) y\(^{-1}\)) than for pan-
Arctic tundra (16 g C m\(^{-2}\) y\(^{-1}\)). Our simulations indicate
that the scaling of C dynamics to a region of arctic tundra
may not represent C dynamics of pan-Arctic tundra
because of the limited spatial variation in climate and
vegetation within a region relative to the pan-Arctic.
Thus, C storage responses for the pan-Arctic should be
evaluated with a methodology that is spatially explicit
across the spatial domain of the pan-Arctic.

Regression-based models, which use empirically de-

derived relationships between climate and C fluxes across a

region to make predictions (see Agren \textit{et al.} 1991),
represent one type of spatially explicit methodology. In
contrast, our simulations rely on a process-based meth-

odology, which simulates the C cycle by using climatically

sensitive equations that describe, in a mechanistic fashion,
the transfer of C between different pools in an ecosystem
(e.g. vegetation and soils). Application of regression-

based models implicitly assume that relationships be-

tween climate and C fluxes developed in one region are
representative of relationships in other regions and that
the relationships do not vary in time. The analysis of
spatial variation in responses of TEM across the Kuparuk
River Basin and the pan-Arctic in four different decades
addresses the validity of these assumptions. The results of
our simulations indicate that responses of C storage show
different climate sensitivities at regional and pan-Arctic
spatial scales and that these sensitivities change across the
temporal scope of the simulations. The different sensitiv-
ities are caused by new combinations of environmental
variables that are experienced by tundra ecosystems
across the spatial domain of the pan-Arctic during the
simulations. Regression-based approaches are only valid
for the combination of environmental variables that affect
ecosystems during the time period over which the studies
to develop the regressions are conducted. Our results
highlight the importance of using a process-based
methodology to evaluate the response of C dynamics
across the spatial domain of the pan-Arctic. Although the
limited spatial variation in climate and vegetation across a
region of arctic tundra may not represent the spatial
variation experienced across tundra of the pan-Arctic, we
emphasize that the real value of regional studies is to
elucidate process-based controls over C dynamics.

\textbf{Reducing uncertainties in projections of pan-Arctic
carbon dynamics}

The results of our study highlight the importance of
incorporating the understanding gained from process-
level studies of C dynamics in a region of arctic tundra
into models that simulate C dynamics in a temporally and
spatially explicit fashion. In this study, we incorporated
information from several studies of C dynamics in arctic
tundra into our simulations (Chapin \textit{et al.} 1980; Shaver &
the Toolik Lake study site, experiments have been
conducted to examine ecosystem responses to perturba-
tions of elevated atmospheric \(\text{CO}_2\) (Oechel & Riechers
1987; Grulke \textit{et al.} 1990; Oechel \textit{et al.} 1992) and to
perturbations involving N fertilization, greenhouse, and
shading (Chapin \textit{et al.} 1995). The model qualitatively
reproduces the responses of ecosystem processes that
have been observed in these experiments (McGuire,
unpubl. data).

Although information from process-level studies of C
dynamics have been incorporated into the simulations of
this study, the ability of a model to reproduce inter-
annual or decadal responses of ecosystems is no
guarantee that the model correctly represents longer
term ecosystem dynamics (see VEMAP Members 1995;
Rastetter 1996). One uncertainty concerns the relative
sensitivity of ecosystem processes to projected changes
in atmospheric \(\text{CO}_2\) and climate. From a series of
additional simulations, we identified that the estimates of
C storage in our simulations are quite sensitive to
assumptions about how vegetation N concentration of
tundra will change in response to changes in \(\text{CO}_2\)

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(see also McGuire et al. 1995b, 1997). This parameter
determines the relative importance of CO₂ changes and
climate changes in influencing responses of pan-Arctic C
storage. Process-based uncertainties have also been
revealed by comparisons among large-scale biogeo-
chemistry models. These comparisons have documented
that although different models present rather consistent
simulations of current conditions, predictions diverge
substantially when climate and CO₂ are altered (VEMAP
Members 1995; pan et al. 1998). Important areas of
divergence include the formulation of the effects of
CO₂ on water and nutrient use and on long-term
coupling of C and N storage.

In addition to assessing process-based uncertainties,
our extrapolation of TEM for the pan-Arctic from 1921 to
2100 also allowed us to evaluate model dynamics in the
context of the input datasets that we developed for this
study. There are substantial uncertainties associated with
the vegetation classification for pan-Arctic tundra in this
study. Our analysis considered two highly aggregated
vegetation types, polar desert/alpine tundra and moist
tundra, which encompass several tundra categories in
circumpolar vegetation classifications that are under
development (Walker, 2000). Also, our analysis did not
distinguish between moist acidic tundra and moist
nonacidic tundra, which appear to have substantially
different C dynamics (Walker et al. 1998). Identification of
uncertainties of C dynamics to projected climate change
in the pan-Arctic would be improved by the application
of parameterizations for the functionally important
vegetation types that occur in the pan-Arctic. Because
process-level understanding is better for some tundra
vegetation types than others, additional studies that
extend understanding of processes in tundra types that
are less-well understood are required before well-tested
parameterizations can be developed. Thus, it is impor-
tant to integrate efforts at classifying pan-Arctic vegeta-
tion with studies of processes in the vegetation types that
comprise the classification.

Another source of uncertainty concerns the role of
topographic variation in controlling C balance of tundra
ecosystems. There is probably greater variation in
ecosystem structure and function along toposequences
within a single region than throughout the latitudinal
range of moist tundra. Thus, topographic controls over
soil moisture and C storage, which we did not consider
in our simulations, may be stronger than the climatic
controls that were considered in our analysis. The
sensitivity of ecosystem processes to soil moisture in
our simulations indicates that topographic controls over
soil moisture are relevant in evaluating the responses of
C storage to projected changes in climate and atmo-
spheric CO₂. An important challenge in future model
development will be to incorporate the interaction
between topographic and climatic controls over soil
moisture in assessing projected responses of tundra C
storage.

The response of vegetation distribution to climate
change in high latitudes represents another uncertainty
in projecting changes in C storage in the pan-Arctic.
In this study we considered primarily responses of
ecosystem function, but C storage in the pan-Arctic is
potentially quite sensitive to the degree that tundra is
replaced by boreal forest (McGuire & Hobbie 1997;
Melillo 1999). Progress in reducing this uncertainty
requires models that consider the temporal dynamics of
the functional and structural responses of C storage at
large spatial scales. To address this uncertainty, we are
presently developing a dynamic model of high-
latitude vegetation that will simultaneously predict the
functional and structural dynamics of C storage in high
latitudes.

There are also substantial uncertainties associated with
the climate datasets of the pan-Arctic that we used in this
study. We used the same methodology to develop the
temperature and precipitation datasets in this study as
was used to develop the datasets for the study of
Amazon River Basin by Tian et al. (1998), in which the
temporal and spatial pattern of temperature and pre-
cipitation variation was successfully represented for El
Niño cycles in recent decades. Because the density of
weather stations in the pan-Arctic is low, there is a great
deal of uncertainty in the datasets of temperature and
precipitation that we used in this study. In general, our
confidence is much higher for the temperature data than
for the precipitation data we used in our simulations of
the pan-Arctic. Because few reliable precipitation data
are available for the pan-Arctic, it is quite possible that
our processing of the available data may result in biased
and inaccurate representation of the temporal and spatial
patterns of precipitation in the pan-Arctic. Our evalua-
tion of the precipitation patterns in our climate datasets
suggest that precipitation and simulated soil moisture
may be overestimated for much of the pan-Arctic in the
later decades of the historical period. The negative
relationship between decomposition and soil moisture
in our simulations suggest that the response of C storage
may be overestimated if soil moisture is overestimated.
Finally, we did not consider temporal variation in
cloudiness or radiation in our simulations, and our
confidence of the long-term spatial patterns in these data
for the pan-Arctic is not high because the data for
developing these datasets are sparse. Gridded datasets
of historical climate are being created for Alaska at 0.5°
resolution using the methodology of Kittel et al. (1997).
A similar effort for the entire pan-Arctic would improve
the ability to assess the responses of C dynamics for pan-
Arctic tundra in a more realistic fashion.

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Conclusion

In this study, we evaluated the temporal and spatial sensitivity of simulated pan-Arctic C storage to temporal and spatial variation in climate across the pan-Arctic. The results of the TEM simulations indicate that while regional studies have the potential to elucidate controls over biome C storage, the limited spatial variation in climate within a region of arctic tundra may not represent the spatial variation in climate experienced across tundra of the pan-Arctic. For reducing uncertainties, our analyses highlight the importance of incorporating the understanding gained from process-level studies of C dynamics in a region of arctic tundra into process-based models that simulate C dynamics in a spatially explicit fashion across the spatial domain of pan-Arctic tundra. There are also substantial uncertainties associated with the vegetation classification and with the climate datasets for pan-Arctic tundra in this study, and our simulations did not consider how topographic controls over soil moisture and vegetation dynamics influence C storage. To reduce uncertainties associated with vegetation classification of pan-Arctic tundra, it is important to integrate efforts at classifying pan-Arctic vegetation with studies of processes in the vegetation types that comprise the classification. A major challenge will be to incorporate topographic controls over soil moisture in assessing the response of C storage for pan-Arctic tundra. The response of vegetation distribution to climate change in high latitudes represents another uncertainty in projecting changes in C storage in the pan-Arctic. Progress in reducing this uncertainty requires models that consider at large spatial scales the temporal dynamics of the functional and structural responses of C storage. Finally, efforts to improve gridded datasets of historical climate for the pan-Arctic would advance the ability to assess the responses of C dynamics for pan-Arctic tundra in a more realistic fashion.

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