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Carbon cycling in extratropical terrestrial ecosystems of the Northern Hemisphere during the 20th century: a modeling analysis of the influences of soil thermal dynamics

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ABSTRACT

There is substantial evidence that soil thermal dynamics are changing in terrestrial ecosystems of the Northern Hemisphere and that these dynamics have implications for the exchange of carbon between terrestrial ecosystems and the atmosphere. To date, large-scale biogeochemical models have been slow to incorporate the effects of soil thermal dynamics on processes that affect carbon exchange with the atmosphere. In this study we incorporated a soil thermal module (STM), appropriate to both permafrost and non-permafrost soils, into a large-scale ecosystem model, version 5.0 of the Terrestrial Ecosystem Model (TEM). We then compared observed regional and seasonal patterns of atmospheric CO_2 to simulations of carbon dynamics for terrestrial ecosystems north of 30°N between TEM 5.0 and an earlier version of TEM (version 4.2) that lacked a STM. The timing of the draw-down of atmospheric CO_2 at the start of the growing season and the degree of draw-down during the growing season were substantially improved by the consideration of soil thermal dynamics. Both versions of TEM indicate that climate variability and change promoted the loss of carbon from temperate ecosystems during the first half of the 20th century, and promoted carbon storage during the second half of the century. The results of the simulations by TEM suggest that land-use change in temperate latitudes (30–60°N) plays a stronger role than climate change in driving trends for increased uptake of carbon in extratropical terrestrial ecosystems (30–90°N) during recent decades. In the 1980s the TEM 5.0 simulation estimated that extratropical terrestrial ecosystems stored 0.55 Pg C yr^{-1}, with 0.24 Pg C yr^{-1} in North America and 0.31 Pg C yr^{-1} in northern Eurasia. From 1990 through 1995 the model simulated that these ecosystems stored 0.90 Pg C yr^{-1}, with 0.27 Pg C yr^{-1} stored in North America and 0.63 Pg C yr^{-1} stored in northern Eurasia. Thus, in comparison to the 1980s, simulated net carbon storage in the 1990s was enhanced by an additional 0.35 Pg C yr^{-1} in extratropical terrestrial ecosystems, with most of the additional storage in northern Eurasia. The carbon storage simulated by TEM 5.0 in the 1980s and 1990s was lower than estimates based on other methodologies, including estimates by atmospheric

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inversion models and remote sensing and inventory analyses. This suggests that other issues besides the role of soil thermal dynamics may be responsible, in part, for the temporal and spatial dynamics of carbon storage of extratropical terrestrial ecosystems. In conclusion, the consideration of soil thermal dynamics and terrestrial cryospheric processes in modeling the global carbon cycle has helped to reduce biases in the simulation of the seasonality of carbon dynamics of extratropical terrestrial ecosystems. This progress should lead to an enhanced ability to clarify the role of other issues that influence carbon dynamics in terrestrial regions that experience seasonal freezing and thawing of soil.

1. Introduction

Globally, terrestrial ecosystems occupy an area of approximately 130 × 10^6 km^2 (McGuire et al., 1995). Approximately 50 million km^2 of this area is affected by the seasonal freezing and thawing of soils in the Northern Hemisphere (Robinson et al., 1995; Kimball et al., 2001; McGuire et al., 2002a, b; Overland et al., 2002). Over the last several hundred years, permafrost conditions in high latitudes have changed, and are likely to continue changing (Lachenbruch et al., 1982; Lachenbruch and Marshall, 1986; Overpeck et al., 1997; Vitt et al., 2000). A growing body of evidence indicates that extratropical terrestrial ecosystems are undergoing substantial changes associated with warming that has been occurring during recent decades (Serreze et al., 2000; McGuire et al., 2002b). Permafrost is currently warming over a substantial part of the Northern Hemisphere (Osterkamp and Romanovsky, 1999; Shender et al., 1999; Romanovsky and Osterkamp, 2001; Romanovsky et al. 2001a, b). Analyses of in situ observations indicate that ice cover on lakes in North America is generally thawing earlier (Magnuson et al., 2000), which suggests that soils are also thawing earlier.

It has been recognized for decades that soil thermal dynamics affects the exchange of carbon between terrestrial ecosystems and the atmosphere (e.g., Kelley et al., 1968; Coyne and Kelley, 1974; Hillman, 1992; Vitt et al., 2000). A number of field-based studies over the last decade have documented both the importance of winter decomposition and freeze–thaw dynamics in the annual carbon budget of extratropical terrestrial ecosystems (Oechel et al., 1997; Jones et al., 1999; Goulden et al., 1998; Grogan and Chapin, 2000). Modeling studies and analyses of satellite-based scatterometer data over the last decade also suggest that soil thermal dynamics play an important role in the dynamics of carbon exchange in extratropical terrestrial ecosystems (Waelbroeck, 1993; Waelbroek and Louis, 1995; Frolking et al., 1996; 1999; Waelbroek et al., 1997; Running et al., 1999; Kimball et al., 2001; McGuire et al., 2000a, b; Clein et al., 2000; 2002). The response of soil carbon storage in high latitudes to continued climate warming is of special concern, as approximately 40% of the world's soil carbon is stored in high-latitude ecosystems (McGuire et al., 1995).

Although there is substantial evidence that soil thermal dynamics are changing in terrestrial ecosystems of the Northern Hemisphere and that these dynamics have implications for the exchange of carbon between terrestrial ecosystems and the atmosphere, large-scale biogeochemical models have been slow to incorporate the effects of soil thermal dynamics on processes that affect carbon dynamics. Most of these models use monthly air temperature, in part, to drive the seasonal dynamics of net primary production and decomposition (e.g., see McGuire et al., 2001). An analysis of changes in carbon storage simulated by four global biogeochemical models in the 20th century has identified that the responses to climate variability and change among the models differ substantially in recent decades. In this study we therefore took the logical step of incorporating a soil thermal module appropriate to both permafrost and non-permafrost soils into a global terrestrial biogeochemical model and parameterized the new model based on data from several intensively studied sites. In particular, we parameterized the soil thermal module based on soil temperature measurements from several Long Term Ecological Research (LTER) sites in the United States. We then applied the model to simulate historical carbon dynamics in terrestrial ecosystems above 30°N, and compared the results of the simulations with a control version of the model to identify the implications of explicitly considering soil thermal dynamics for carbon dynamics of extratropical terrestrial ecosystems. To determine if the consideration of soil thermal dynamics improved the simulation of carbon exchange with the atmosphere, we also evaluated the results of the simulations in the context of observed seasonal atmospheric CO_2 dynamics, and in the context of estimates of carbon exchange based on inverse modeling and on remote sensing and forest inventory analyses.

2. Methods

2.1. Model description

To provide the capability to explicitly consider the effects of soil thermal dynamics and terrestrial cryospheric processes on large-scale carbon dynamics of terrestrial ecosystems, we developed version 5.0 (Fig. 1a) of the Terrestrial Ecosystem Model (TEM) by coupling version 4.2 of TEM (McGuire et al., 2001) with a soil thermal module (STM, Zhuang et al., 2001); TEM 4.2 is the control version of TEM used in this study. The new version of TEM, like its predecessors, is a highly aggregated large-scale biogeochemical model that uses spatially referenced information on climate, elevation, soils and vegetation to simulate carbon and nitrogen dynamics of global terrestrial ecosystems (Fig. 1b). Data sets of historical CO_2, climate and cropland extent were used to drive the models at 0.5° resolution (latitude by longitude). TEM

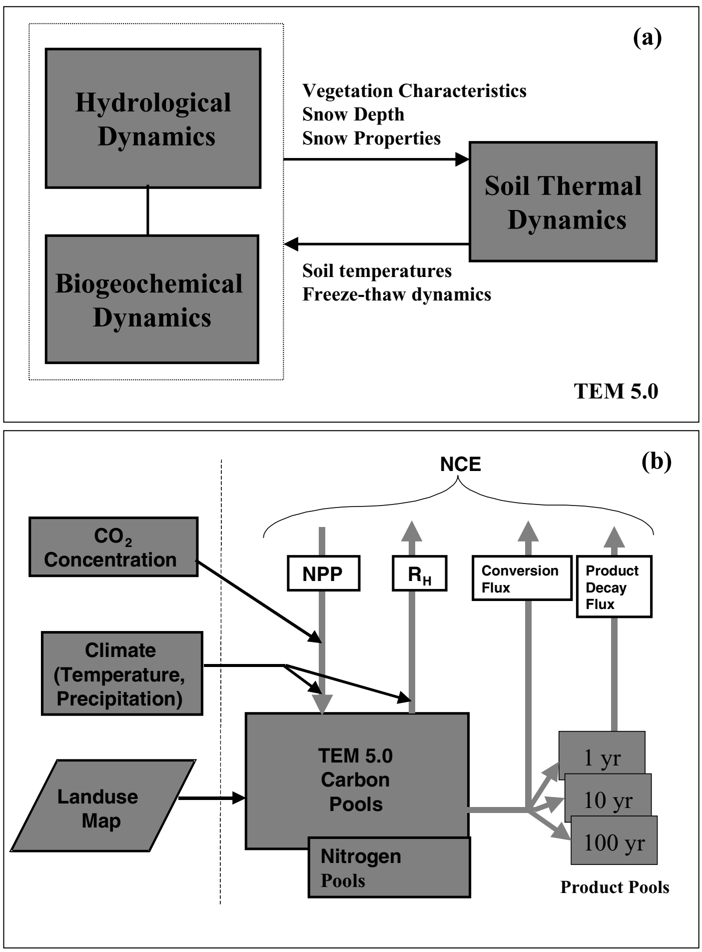

Fig. 1. (a) The structure of TEM 5.0 includes (1) hydrological dynamics based on a Water Balance Model (WBM, Vorosmarty et al., 1989), biogeochemistry dynamics based on the Terrestrial Ecosystem Model (TEM 4.2, McGuire et al., 2001), and soil thermal dynamics based on the Soil Thermal Module (STM, Zhuang et al., 2001). Among the three components, the STM receives vegetation characteristics from TEM, receives snow depth and snow properties from the WBM, and provides simulated soil temperatures and freeze–thaw dynamics to TEM to drive ecosystem processes. (b) Overview of the simulation protocol implemented by TEM 5.0 in this study to assess the concurrent effects of increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment during the 20th century.

estimates net primary production (NPP) and heterotrophic respiration (R_H). The conversion flux is the simulated release of CO_2 associated with the clearing of land for agriculture, i.e., the burning of slash and fuel wood. Biomass harvested from land as a result of conversion to agriculture or subsequent cultivation decays to the atmosphere from three pools with different residence times: a 1 yr product pool (decay of agricultural products), a 10 yr product pool (paper and paper products) and a 100 yr pool (lumber and long-lasting products). The flux NCE is the net exchange of carbon between the ecosystem and the atmosphere where NCE $= R_H -$ NPP $+$ Conversion flux $+$ Product decay flux. The STM is based on the Goodrich model (Goodrich 1976; 1978a, b), and has the capability of representing soil thermal dynamics in both permafrost and non-permafrost soils (Zhuang et al., 2001; 2002). Our modifications of the STM included an improved representation of the effects of snow depth on the soil thermal regime. As part of coupling the two models, we revised the calculations of heterotrophic respiration (R_H, i.e., decomposition) and net nitrogen mineralization in TEM so that these important soil processes were functions of soil temperature rather than air temperature. However, the model does not explicitly track or consider the effects of the age of soil organic matter in estimating the decomposition of soil organic matter. We also added calculations to better represent the effects of freeze–thaw dynamics on gross primary production.

2.1.1. Effects of snow characteristics on soil thermal regime. Different types of snow cover have different thermal properties, which can influence the soil thermal dynamics of terrestrial ecosystems. For example, wind-packed high-density snow that is typical of tundra regions has high thermal conductivity and less insulative effects on the soil thermal regime in comparison to snow cover in the boreal forest. In the previous version of the STM (Zhuang et al., 2001), a constant snow thermal conductivity was prescribed for each vegetation type, and snow depth was estimated through combining a simulated snow water equivalent with a prescribed snow density. To better characterize the soil thermal regime of the terrestrial ecosystems affected by seasonal snow cover, a snow classification system for seasonal snow cover (Sturm and Holmgren, 1995) was implemented to dynamically estimate the snow depth and the snow thermal conductivity. The classification system includes snow cover types for lowland tundra, alpine tundra, taiga forest, maritime forest, prairie grasslands and for ecosystems that experience ephemeral snow cover, where each class was defined by a unique ensemble of textural and stratigraphic characteristics, including the sequence of snow layers, their thickness, density and the crystal morphology and grain characteristics within each layer. A variety of snow densities are associated with different snow cover classifications (Liston and Pielke, 2000). These snow densities were used to estimate the thermal conductivity, which was calculated (Sturm et al., 1997) as follows:

$$k_s = 10^{(2.650\rho - 1.652)} \tag{1}$$

where k_s is snow thermal conductivity (W m^{-1} K^{-1}) and ρ is snow density (g cm^{-3}). Snow depth was estimated as follows:

$$D_s = SWE/\rho \tag{2}$$

where D_s is snow depth (m) and SWE is snow-water-equivalent depth (m), which is simulated by the hydrological dynamics module of TEM 5.0 (Fig. 1a).

2.1.2. Effects of freeze–thaw dynamics on gross primary production. While soil thermal dynamics directly affect ecosystem processes like decomposition of soil organic matter and the mineralization of soil organic nitrogen, it is also important to consider the effects of freeze–thaw dynamics on carbon uptake at sub-monthly temporal resolution, because environmental conditions change so rapidly during spring thaw. The timing of spring thaw and the duration of the growing season are strongly linked to the carbon balance of high-latitude ecosystems (Goulden et al., 1997; Frolking et al., 1996; Frolking, 1997). We introduced into TEM 5.0 an index of sub-monthly freeze–thaw, which represents the proportion of a specific month in which the ground is thawed, to better account for the effects of freeze–thaw dynamics on carbon uptake in terrestrial ecosystems (Table 1). Our previous experience with the STM for several major ecosystem types in the Northern Hemisphere indicated that the time of thaw at 10 cm showed good agreement with the onset of photosynthesis. Therefore, we calculated the freeze–thaw index, f(FT), based on simulated soil temperatures at a depth of 10 cm. The index varies from 0.0 to 1.0 and influences the ability of the vegetation to take up atmospheric CO_2 through the calculation of gross primary production (GPP) in the model. In TEM 5.0 we incorporated the freeze–thaw index into

Table 1. *Formulae used in TEM 5.0 to calculate the freeze–thaw index in the present month*

Combinations	Conditions of three consecutive months	Formulae of freeze–thaw indexes
C_1[a]	$+++$[b]	1.0[c]
C_2	$++-$	$1-[T_m/(T_m - T_{m-1})]$
C_3	$+--$	$1-[T_{m+1}/(T_{m+1} - T_m)]$
C_4	$---$	0.0
C_5	$-+-$	$\{1-[T_m/(T_m - T_{m-1})]\} + [T_m/(T_m - T_{m+1})]\}/2.0$
C_6	$-++$	$T_m/(T_m - T_{m+1})$
C_7	$--+$	$T_{m-1}/(T_{m-1} - T_m)$
C_8	$+-+$	$([T_{m-1}/(T_{m-1} - T_m)] + \{1-(T_{m+1/}(T_{m+1} - T_m)]\})/2.0$

[a] $C_i$represents a particular combination of freeze and thaw conditions during three consecutive months,
[b] Positive or negative symbol indicates the sign of previous, present, and the next monthly soil temperature, respectively
[c] T_m, T_{m-1} and T_{m+1} represent soil temperatures at 10 cm depth for present, previous and the next month, respectively. If the same value of soil temperature is simulated in two consecutive months, we specify the soil temperature difference between those two months to a non-zero value to keep the above formulae valid without losing biological meaning. Similarly, if soil temperature is 0 °C for a specific month, the value is forced to 0.001 °C.

the calculation of GPP:

$$\mathrm{GPP} = C_{\max} f(\mathrm{PAR}) f(\mathrm{PHENOLOGY}) \times f(\mathrm{FOLIAGE}) f(T) f(C_{\mathrm{a}}, G_{\mathrm{v}}) f(\mathrm{NA}) f(\mathrm{FT}) \quad (3)$$

where $C_{\max}$ is the maximum rate of C assimilation, PAR is photosynthetically active radiation, and f(PHENOLOGY) is monthly leaf area relative to leaf area during the month of maximum leaf area and depends on monthly estimated evapotranspiration (Raich et al., 1991). The function f(FOLIAGE) is a scalar function that ranges from 0.0 to 1.0 and represents the ratio of canopy leaf biomass relative to maximum leaf biomass (Zhuang et al., 2002), T is monthly air temperature, C_{a} is atmospheric CO_2 concentration, G_{v} is relative canopy conductance, and NA is nitrogen availability. The effects of elevated atmospheric CO_2 directly affect $f(C_{\mathrm{a}}, G_{\mathrm{v}})$ by altering the intercellular CO_2 of the canopy (McGuire et al., 1997; Pan et al., 1998). The function f(NA) models the limiting effects of plant nitrogen status on GPP (McGuire et al., 1992; Pan et al., 1998). Compared to the control version of TEM, the function f(FT) is the only new factor in the GPP calculation of TEM 5.0. Additional details about the calculation of GPP can be found in Tian et al. (1999).

2.2. *Model parameterization*

The variables and parameters of the STM are described in detail by Zhuang et al. (2001). We parameterized the soil thermal dynamics of TEM 5.0 for several different vegetation types based on soil temperature measurements at LTER sites in the United States (Table 2). The parameterization was conducted to minimize the differences between the simulated and measured soil temperatures at different soil depths for those sites (Fig. 2). The values of the parameters and the depth steps within different soil layers used for each of the sites are compiled in Table 3.

Parameters in TEM may be specific to different vegetation types, specific to different soil textures, or constant for all vegetation types and soil textures. Most of the parameters in TEM are assigned values derived from the literature, but some parameters are calibrated to the carbon and nitrogen pools and fluxes of intensively studied sites (see Raich et al., 1991 and McGuire et al., 1992 for more details). The calibration procedure estimates the rate limiting parameters for gross primary production [$C_{\max}$ in eq. (3)], autotrophic respiration, heterotrophic respiration, plant nitrogen uptake and soil nitrogen immobilization in the context of other TEM parameters, which were not altered from values used in previous versions of the model. Thus, the new parameterization accounts for the effects of using soil temperature instead of air temperature to drive below-ground processes (heterotrophic respiration and net nitrogen mineralization) and the effects of incorporating freeze–thaw dynamics to constrain the timing of carbon uptake through photosynthesis. Both TEM 5.0 and the control version of TEM were parameterized with atmospheric CO_2 concentration set to 280 ppmv, which is approximately the level of CO_2

Table 2. *Site descriptions, soil characteristics, driving data and measured data used to calibrate TEM*

Site name	Location (Lon./Lat.)	Elevation (m)	Vegetation type	Soil characteristics	Driving climate data	Observed data	Sources and comments
Jornada (USA)	106.78° W/ 32.53° N	1360	Mixed grassland/ sub-shrublands	Litter under a shrub widely scattered, little organic layer, moss thickness may reach to 3–6 cm	Measured air temperature and precipitation (1983–1999)	Soil temperature at 5 cm depth (1995–1999)	Jornada LTER web site, John Anderson (personal communication)
Deadhorse (Alaska)	148.47° W/ 70.1° N	17	Moist non-acidic tundra	Peat soil about 23 cm, silt layer about 70 cm, and then sand and silt, gravel till 16 m. Volumetric water content are 60 and 45% for peat and silt, respectively	Air temperature and precipitation (1984–1997). See http://www.ncdc.Noaa.gov.	Soil temperature at 0.12, 0.22, 0.32, and 0.42 m (1992–1994)	Romanovsky and Osterkamp (1997); Zhang et al. (1997)
Harvard Forest (USA)	72.1° W/ 42.53° N	340	Mixed hardwood and conifer forests	Rooting depth is about 50 cm	Measured air temperature (1995–1999). The precipitation from McGuire et al. (2001)	Soil temperature at soil surface, 20 and 50 cm depth (1992–1993)	Eric Davidson (personal Communication)
Konza Prairie (USA)	96.58° W/ 39.08° N	320–444	Tallgrass prairie	Rocky soils characteristics	Measured air temperature and precipitation (1993–1996)	Soil temperature at depth 25 cm (1993–1996)	See http:// www.ksu.edu/konza
Luquillo (Puerto Rico)	65.72° W/ 18.32° N	153	Savana tropical forests	Deep clays, well weathered but nutrient rich, are derived from volcanoclastic andesitic sandstones and siltstones (see Soil Survey Staff 1995)	Measured air temperature of 1997. Precipitation from McGuire et al. (2001)	Soil temperature at 10–15 cm of 1997	Brown et al. (1983); Garcia et al. (1996) See www.fs.fed.us
Arctic Tundra (Alaska)	149.72° W/ 68.63° N	760	Tussock tundra	Soils are moist, 0–30 cm thick organic mat, underlain by a silty mineral soil. Continuous permafrost, the maximum depth of thaw is 30–50 cm	See Zhuang et al. (2001)	See Zhuang et al. (2001)	Chapin and Shaver (1985); Shaver and Chapin (1986), http://ecosystems.mbl.edu/ ARC
Bonanza Creek (Alaska)	148.0° W/ 64.8° N	120	Conifer forest	Discontinous permafrost, moss plus organic is about about 40 cm, mineral soil could be down to 1 m	Air temperature and precipitation are from weather station (1983–2000)	Temperatures of soil surface and at 15, 30, 60 and 90 cm	Roy E. Erickson (Pers. Commun.). See www.lter.uaf.edu

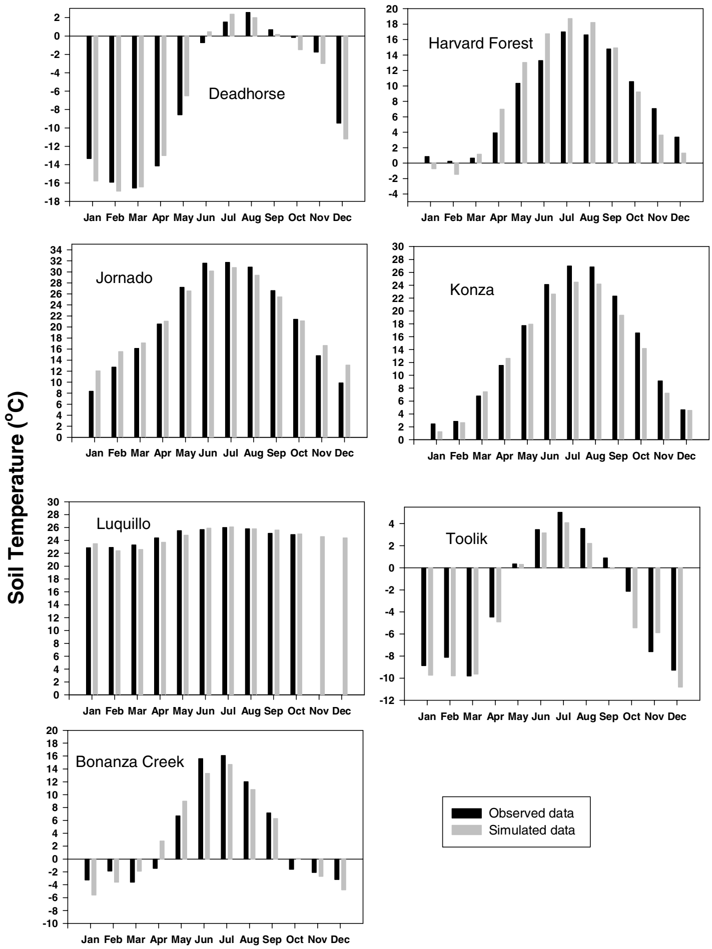

Fig. 2. Comparisons of monthly soil temperatures between observations and simulations by TEM 5.0. The temperatures were compared at 20 cm soil depth for the Deadhorse, Bonanza Creek, Harvard Forest and the Toolik sites, at 5 cm soil depth for the Jornada site, at 15 cm depth for the Luquillo site, and at 25 cm depth for the Konza site. For the descriptions of these sites see Table 2.

that was used to initialize the model simulations in this study. This differed from the parameterization of TEM 4.2 used by McGuire et al. (2001), which was parameterized for an atmospheric CO_2 concentration of 340 ppmv. The definition of parameters used in TEM has been documented in a number of studies (Raich et al., 1991; McGuire et al., 1992; Tian et al., 1999).

2.3. *Model application*

2.3.1. Input datasets. To apply TEM 5.0 to make spatially and temporally explicit estimates of ecosystem processes in this study, we used the same input data sets as were used to drive TEM 4.2 in McGuire et al. (2001). These input data sets are important for directly affecting processes in the model (e.g., the effects of soil temperature on heterotrophic respiration) and for defining the parameters that are specific to vegetation types and soil textures. We used a potential vegetation data set similar to that described in Melillo et al. (1993) to run the model to equilibrium prior to driving the model with transient changes in atmospheric CO_2, climate or land use. Soil texture, elevation and cloudiness did not vary in any of the simulations. The transient input data included historical atmospheric CO_2 concentrations (Etheridge et al., 1996; Keeling

Table 3. *Parameterization of TEM with measurements of soil temperatures at Deadhorse Jornada, Luquillo, Bonanza Creek, Harvard Forest, Konza and Toolik sites*[a]

Variables	Jornado	Deadhorse	Harvard Forest	Konza Prairie	Luquillo	Toolik	Bonanza Creek	Unit
Thickness of soil layer 1	0.10 (0.05)[b]	0.22 (0.11)	0.10 (0.10)	0.05 (0.05)	0.10 (0.05)	0.20 (0.10)	0.20 (0.05)	m
Thickness of soil layer 2	1.00 (0.10)	0.50 (0.10)	1.00 (0.10)	2.00 (0.15)	1.00 (0.10)	0.60 (0.15)	0.35 (0.10)	m
Thickness of soil layer 3	1.00 (0.10)	1.00 (0.20)	1.00 (0.20)	1.00 (0.20)	1.00 (0.20)	0.90 (0.30)	1.00 (0.20)	m
Thickness of soil layer 4	6.00 (0.50)	3.00 (0.50)	5.00 (0.50)	3.00 (0.50)	10.0 (0.50)	4.00 (0.50)	5.00 (0.50)	m
Thawed thermal conductivity of layer 1	0.25	0.09	0.75	2.50	0.55	0.30	0.25	$W\ m^{-1}\ K^{-1}$
Frozen thermal conductivity of layer 1	0.36	1.20	0.46	2.01	0.36	0.56	0.15	$W\ m^{-1}\ K^{-1}$
Thawed thermal conductivity of layer 2	0.70	0.20	0.70	0.20	0.70	0.70	0.50	$W\ m^{-1}\ K^{-1}$
Frozen thermal conductivity of layer 2	1.65	1.25	1.60	1.60	1.60	1.50	1.00	$W\ m^{-1}\ K^{-1}$
Thawed thermal conductivity of layer 3	1.15	1.10	1.40	1.20	1.50	1.00	1.20	$W\ m^{-1}\ K^{-1}$
Frozen thermal conductivity of layer 3	2.05	2.00	2.30	2.10	2.20	2.00	2.10	$W\ m^{-1}\ K^{-1}$
Thawed thermal conductivity of layer 4	1.15	1.10	1.40	1.20	1.50	1.00	1.20	$W\ m^{-1}\ K^{-1}$
Frozen thermal conductivity of layer 4	2.05	2.00	2.30	2.10	2.20	2.00	2.10	$W\ m^{-1}\ K^{-1}$
Water content of layer 1	0.54	0.34	0.64	0.14	0.64	0.35	0.18	Volumetric %
Water content of soil layer 2	0.65	0.43	0.65	0.65	0.65	0.10	0.20	Volumetric %
Water content of soil layer 3	0.43	0.45	0.43	0.43	0.43	0.43	0.43	Volumetric %
Soil water content of layer 4	0.43	0.43	0.43	0.43	0.43	0.43	0.43	Volumetric %
Thawed volumetric heat capacity of layer 1	1.50	1.70	1.70	2.40	1.70	1.50	1.70	$MJ\ m^{-1}\ K^{-1}$
Frozen volumetric heat capacity of layer 1	1.20	1.50	1.50	2.30	1.50	1.20	1.50	$MJ\ m^{-1}\ K^{-1}$
Thawed volumetric heat capacity of layer 2	2.60	1.70	2.60	2.60	2.60	1.30	2.60	$MJ\ m^{-1}\ K^{-1}$
Frozen volumetric heat capacity of layer 2	2.40	1.50	2.40	2.40	2.40	1.20	2.40	$MJ\ m^{-1}\ K^{-1}$
Thawed volumetric heat capacity of layer 3	3.00	3.00	3.40	3.20	3.30	2.90	3.10	$MJ\ m^{-1}\ K^{-1}$
Frozen volumetric heat capacity of layer 3	1.60	1.60	1.90	1.80	1.80	1.50	1.70	$MJ\ m^{-1}\ K^{-1}$
Thawed volumetric heat capacity of layer 4	3.00	3.00	3.40	3.20	3.30	2.90	3.10	$MJ\ m^{-1}\ K^{-1}$
Frozen volumetric heat capacity of layer4	1.60	1.60	1.90	1.80	1.80	1.50	1.70	$MJ\ m^{-1}\ K^{-1}$

[a]See Table 1 for more information.
[b]The numerical value following the thickness of each layer was the depth step of the simulation.

et al., 1995, updated). The data sets describing historical changes in monthly air temperature and precipitation were gridded at 0.5° × 0.5° spatial resolution based on data sets of Jones (1994, updated) and Hulme (1995, updated). To represent historical land use in our simulations, we used the same data sets for agricultural establishment and abandonment and for relative agricultural productivity as were used in McGuire et al. (2001).

2.3.2. The simulations. To examine the relative roles of CO_2 fertilization, climate variability, and land use change on terrestrial carbon dynamics with consideration of soil thermal dynamics, as per McGuire et al. (2001) we conducted three sets of simulations from 1860 to 1995 with both TEM 5.0 and the control version of TEM. The first simulation (S1) allowed atmospheric CO_2 to change from year to year and treated the climate as constant from year to year. The second simulation (S2) is similar to the S1 simulation except that historical transient temperature and precipitation were also used to drive the simulation. In addition to changes in atmospheric CO_2 and climate, the third simulation (S3) used prescribed changes in land cover associated with agricultural establishment and abandonment, which allowed potential vegetation to be converted to cropland and allowed cropland to be converted to potential vegetation (McGuire et al., 2001).

For each of the simulations, the model simulated net primary production (NPP), heterotrophic respiration (R_H) and stocks of vegetation and soil carbon. In the S3 simulation, TEM also simulates the emissions associated with the conversion of potential vegetation to agriculture (E_C) and emissions associated with the decay of agricultural, wood and fiber products (E_P) (Fig. 1b; see McGuire et al., 2001). In the S1 and S2 simulations, net carbon exchange (NCE) is calculated as $R_H -$ NPP, while in the S3 simulation, NCE is calculated as the $R_H + E_C + E_P -$ NPP. Thus, a positive NCE represents a source of CO_2 from terrestrial ecosystems to the atmosphere, while a negative NCE represents a CO_2 sink from the atmosphere to terrestrial ecosystems.

2.4. Model evaluation

2.4.1. Seasonal carbon exchange and effects on atmospheric CO_2 concentrations. To examine the effects of soil thermal dynamics on seasonal carbon dynamics, we compared the simulated seasonal dynamics of NCE, NPP and R_H during the 1980s for both temperate zone ecosystems (30–60°N) and high-latitude ecosystems (60–90°N) between TEM 5.0 and the application of control version of TEM. Similar to Dargaville et al. (2002b), we used the results of the S2 simulations in this analysis. To simulate atmospheric CO_2 concentrations at various CO_2 monitoring stations, we provided monthly estimates of NCE from the S2 simulations for the period from 1982 through 1995 to the Model of Atmospheric Transport and Chemistry (MATCH; Rasch et al., 1997; Mahowald et al., 1997). Observed atmospheric CO_2 concentrations from the 15 Climate Monitoring and Diagnostic Laboratory (CMDL) sites were compared with estimated CO_2 concentration based on the S2 simulations of the different versions of TEM (see also Dargaville et al., 2002b). To evaluate how well the TEM simulations reproduced the observed seasonal signal of atmospheric CO_2 at a monitoring station, we calculated the root mean-squared error (RMSE) between the observed mean concentrations of CO_2 from available data in the 1983–1992 period with the mean concentrations based on the S2 simulations.

2.4.2. Decadal changes in seasonal carbon dynamics. The analysis of the TEM 4.2 simulations of McGuire et al. (2001) suggested that land use change was more important than climate variability and change in affecting seasonal carbon dynamics over the last several decades. To evaluate the relative roles of soil thermal dynamics and land use change in affecting the seasonal dynamics of carbon exchange during the last several decades, we compared the seasonal pattern of cumulative NCE between the S2 and the S3 simulations of TEM 5.0 and the control version of TEM. As E_C and E_P in the S3 simulations are simulated with annual resolution, we evenly distributed these fluxes over the months of the year to calculate cumulative seasonal NCE for the S3 simulations. The appropriateness of assuming that these fluxes are evenly distributed throughout the year is evaluated in a separate study (Zhuang et al., in preparation). We focused our analysis of cumulative NCE on the 1960s, 1970s, and 1980s and examined the timing of growing season and the carbon sink and source activities in both temperate and high-latitude regions.

2.4.3. Changes in carbon storage over the past century and during the 1980s and 1990s. To evaluate how the consideration of soil thermal dynamics influenced carbon storage during the 20th century, we analyzed how increasing atmospheric CO_2, climate change and variability, and land-use change contributed to simulated changes in carbon storage between the two versions of TEM for three periods: 1920–1957, 1958–1995 and 1980–1995. The contributions of CO_2 fertilization, climate change and variability and land-use change to changes in carbon storage were determined through use of the estimates of NCE simulated among the S1, S2 and S3 for each version of TEM. The effect of CO_2 fertilization was defined as NCE of the S1 simulations, the effect of climate variability and change was approximated by the differences in NCE between the S2 and the S1 simulations, and the effect of land use change was approximated by the difference in NCE between the S3 and S2 simulations. Note that this method of partitioning actually estimates the marginal effects of climate variability and change and the marginal effects of land use change (McGuire et al., 2001). For example, the estimate of the effect of climate includes interactions between changes in atmospheric CO_2 and climate. We also split the 1980–1995 period into two sub-periods (1980–1989 and 1990–1995) and analyzed differences in simulated changes in carbon storage between North America and northern Eurasia. We evaluated how soil thermal dynamics might influence decadal variability between the 1980s and 1990s and spatial patterns of carbon storage by comparing the changes in carbon storage simulated by the two versions of TEM with (1) analyses based on an ensemble of simulation experiments among atmospheric inverse models (e.g., Prentice et al., 2001; Schimel et al., 2001) and (2) analyses based on remote sensing and inventory data (e.g., Myneni et al., 2001; Goodale et al., 2002). For any analyses that reported estimates in units of biomass instead of carbon, we multiplied biomass by 0.475 to express the estimates in units of carbon, a conversion factor that we routinely use for this purpose (see Raich et al., 1991).

3. Results

3.1. *Seasonal carbon exchange and effects on atmospheric CO_2 concentrations*

The consideration of soil thermal dynamics in the TEM 5.0 simulations substantially affected the mean seasonality of carbon exchange between extratropical terrestrial ecosystems and the atmosphere during the 1980s (Fig. 3). In comparison to the control version of TEM, TEM 5.0 simulated that net uptake of carbon in the spring was depressed in temperate latitudes during May (Fig. 3a) and in high latitudes during June (Fig. 3b). In temperate latitudes, the combination of a relative decrease in NPP (Fig. 3c) and a relative increase in R_H (Fig. 3e) was responsible for reduced carbon uptake during May in the TEM 5.0 simulation. In high latitudes, a similar relative decrease in NPP (Fig. 3d) and R_H (Fig. 3f) was responsible for reduced carbon uptake during June in the TEM 5.0 simulation. While the net uptake of carbon was depressed in the spring, the uptake of carbon during the rest of summer was enhanced from June through September in temperate latitudes (Fig. 3a) and during July and August in high latitudes (Fig. 3b), with a shift in peak carbon uptake from May to June in temperate latitudes and from June to July in high latitudes. In temperate latitudes, the combination of a relative in increase in NPP (Fig. 3c) and a relative decrease in R_H (Fig. 3e) was responsible for the higher carbon uptake from June through September (Fig. 3a). In contrast, a relative increase in NPP of high latitudes in July and August (Fig. 3d) was primarily responsible for higher uptake (Fig. 3b), as simulated R_H was also higher during these months (Fig. 3f). Thus, in temperate latitudes the effects of soil thermal dynamics on both NPP and R_H were responsible for differences in the seasonal dynamics of net carbon uptake between our simulations, while in high latitudes the effects of soil thermal dynamics on NPP were primarily responsible for differences.

The effects of soil thermal dynamics in TEM 5.0 on the simulated seasonal dynamics of carbon exchange between extratropical terrestrial ecosystems and the atmosphere influenced the seasonality of atmospheric CO_2 concentrations throughout the Northern Hemisphere (Fig. 4). In comparison to the control version of TEM, the coupling of seasonal carbon exchange from TEM 5.0 with the atmospheric transport model MATCH substantially improved the simulated magnitude and timing of atmospheric CO_2 draw down during the growing season for many of the monitoring stations in the Northern Hemisphere (Fig. 4); the root mean squared error between simulated and observed was substantially reduced for all of the Northern Hemisphere monitoring stations we examined (STM through GMI in Table 4). For most stations, the seasonal concentration anomalies of atmospheric CO_2 derived from the TEM 5.0 simulations were within one standard deviation of the observations during the Northern Hemisphere growing season (Fig. 4). While the late winter CO_2 concentration anomalies were overestimated for several stations in the TEM 5.0 simulations (Fig. 4; e.g., see MBC, BRW, STM, CMO and KEY), these biases were more than compensated by improvements in simulating concentration anomalies during the growing season. Among

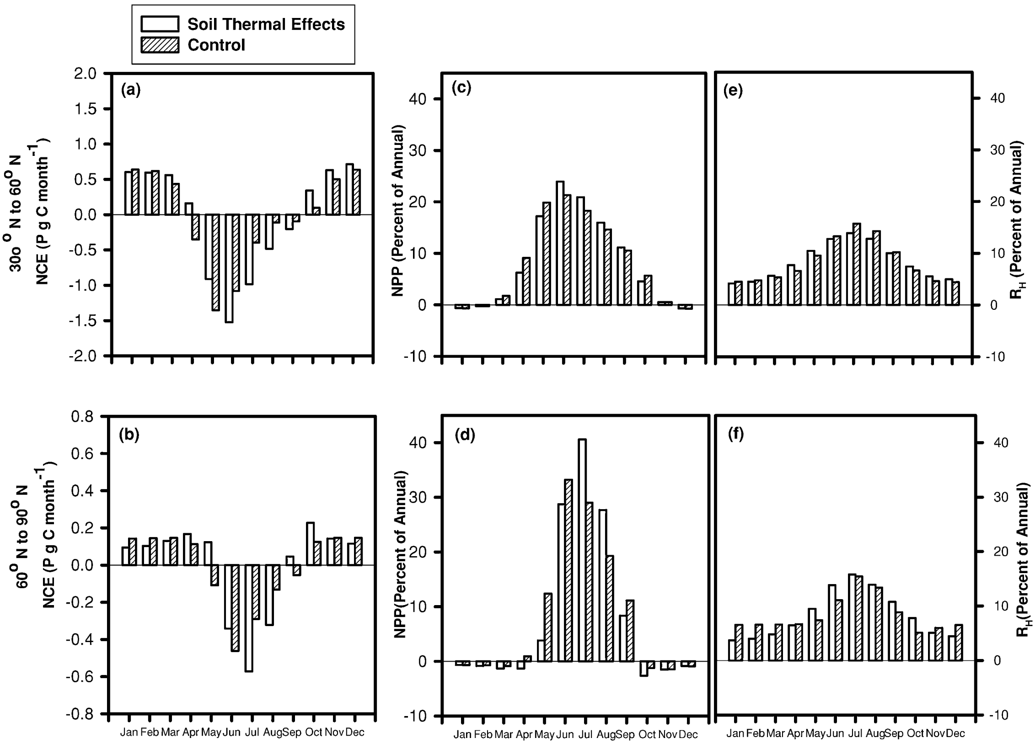

Fig. 3. Monthly simulated net carbon exchange (NCE, left panels) and monthly relative net primary production (NPP, center panels) and heterotrophic respiration (R_H, right panels) as estimated by TEM 5.0 and its control simulations for 30–60°N (top panels: a, c and e) and 60–90°N (bottom panels: b, d and f). The simulations are from S2 simulations of the two versions of TEM. The TEM 5.0 simulations are indicated with open bars, and control simulations with hatched bars.

the 15 stations we evaluated, the root mean squared errors (RMSEs) derived from the TEM 5.0 simulation were significantly reduced in comparison to those from the control simulation at an alpha level of 0.10 (paired sample t-test: $t = 1.89, P = 0.078, N = 15$). For six temperate and high-latitude stations (MBC, BRW, STM, CBA, MLO and KUM) the root mean squared error (RMSE) between simulations and observations was significantly smaller for the TEM 5.0 simulation in comparison to the control simulation. While the RMSEs of the TEM 5.0 simulations were not significantly different from the control simulations for the remaining stations we evaluated, they were generally smaller except for the station at Cape Meares in Oregon (CMO) and three Southern Hemisphere stations (SMO, PSA and SPO).

3.2. Decadal changes in seasonal carbon dynamics

In comparison with the control S2 simulation, the S2 simulation by TEM 5.0 is characterized by a later zero crossing point of positive carbon storage in both temperate and high latitudes in all three decades (Figs. 5a and 5b), which is consistent with the analyses of section 3.1. Both versions of TEM indicate that there was a very weak decadal-scale trend for an earlier zero-crossing point of positive carbon gain during the year that occurred primarily between the 1960s and 1970s in both temperate and high latitudes (Figs. 5a and 5b). In contrast, both S3 simulations of TEM indicate a substantial decadal-scale trend for an earlier zero-crossing point in temperate latitudes (Fig. 5c), with a stronger trend between the 1970s and 1980s than between the 1960s and 1970s. Similar to the S2 simulations, both S3 simulations of TEM indicate that the trends for an earlier crossing point in high latitudes were weak and occurred primarily between the 1960s and the 1970s, with little difference between the 1970s and 1980s (Fig. 5d). These results simulated by TEM suggest that land-use change in temperate latitudes plays a stronger role than climate change in

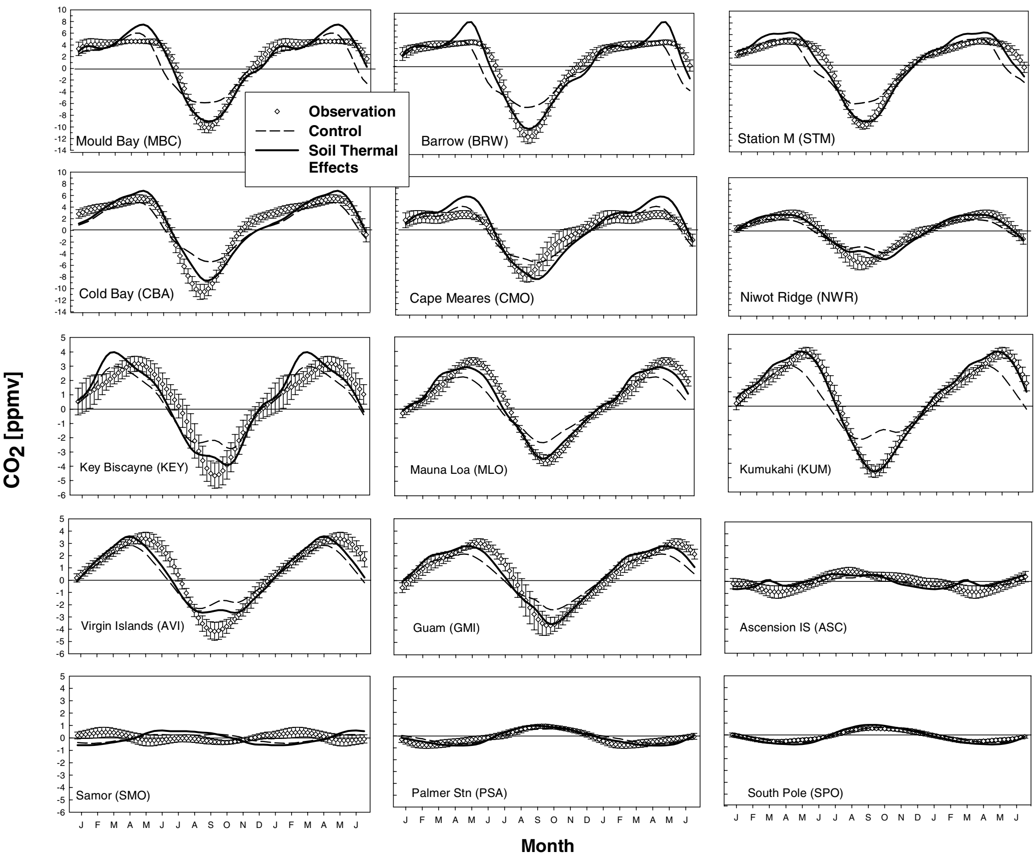

Fig. 4. Comparisons between the observed seasonal cycle of CO_2 and simulated seasonal cycle for 15 monitoring stations of the NOAA/CMDL network. The mean and standard deviation from 1982 to 1995 are shown for the observed data. The simulated CO_2 concentrations were estimated by providing the monthly NCE estimates of the TEM 5.0 simulation (soil thermal effects, solid line) and the TEM 4.2 simulation (control, dashed line) to the Model of Atmosphere and Transport Chemistry (MATCH). The first 6 months of each cycle are displayed twice to reveal the annual variation more clearly.

driving decadal-scale trends for increased uptake of carbon in extratropical terrestrial ecosystems.

3.3. *Changes in carbon storage over the past century and during the 1980s and 1990s*

Both applications of the control version of TEM and TEM 5.0 indicate that extratropical terrestrial ecosystems generally lost carbon between 1920 and 1957 (period 1; Table 5) and stored carbon from 1958 to 1995 (period 2; Table 5). Carbon losses in period 1 (Fig. 6a, Table 5) were primarily caused by changes in land use that occurred in the temperate zone, while carbon gains in period 2 (Fig. 6b, Table 5) were primarily caused by increases in atmospheric CO_2 and changes in climate. Climate variability and change had minor effects on net carbon storage in period 1, but substantially enhanced carbon storage in period 2. In comparison to the control simulation, TEM 5.0 simulated slighter low carbon losses in period 1 (1.1 Pg C; Table 5) and greater carbon uptake in period 2 (1.6 Pg C, Table 5). While the consideration of soil thermal dynamics had minor influences on changes in carbon storage during the 20th century, it tended to depress carbon losses and to enhance carbon gains.

From 1980 to 1995, both applications of TEM indicate that extratropical terrestrial ecosystems stored carbon (Table 6), with the largest areas of carbon sequestration in northern Eurasia and the United States (Fig. 6c). While both increasing atmospheric CO_2 and

Table 4. *The root mean squared errors (RMSE) between simulations and observations of atmospheric CO_2 concentration at the monitoring stations of NOAA/CMDL network*

Monitoring stations[a]	Soil Thermal effects[b]	Control[c]
STM	1.5	1.9
BRW	1.7	2.4
CBA	1.8	2.3
MBC	1.4	2.1
CMO	1.8	1.2
NWR	1.0	1.1
KEY	1.0	1.0
MLO	0.6	0.9
KUM	0.5	0.9
AVI	1.0	1.2
GMI	0.6	0.9
ASC	0.4	0.4
SMO	0.6	0.5
PSA	0.8	0.6
SPO	0.2	0.1

[a]See Fig. 4 for the full name of stations.
[b]RMSE is calculated between the simulated and observed CO_2 for each stations with 48 point CO_2 data; for detailed procedures, see Dargaville et al. (2002a). The simulated CO_2 with soil thermal effects was determined by coupling carbon exchange simulated by TEM 5.0 to MATCH.
[c]RMSE is calculated between the simulated and observed CO_2 for each stations with 48 point CO_2 data. The simulated CO_2 associated with the control column was determined by coupling the carbon exchange simulated by TEM 4.2 to MATCH.

climate variability and change led to carbon storage in both temperate and high latitudes, land-use change led to carbon storage in temperate latitudes and had no net effect in high latitudes (Table 6). From 1980 to 1995, the TEM 5.0 simulation indicates that extratropical terrestrial ecosystems stored 0.68 Pg C yr^{-1}, which is slightly greater than the storage indicated by the control simulation (0.61 Pg C yr^{-1}). In the TEM 5.0 simulation CO_2 fertilization, climate variability and change, and land-use change contributed approximately 60%, 25% and 15%, respectively, to carbon sequestration from 1980 to 1995 (Table 6).

During the 1980s and 1990s TEM 5.0 estimated that carbon storage in vegetation biomass was responsible for 61% of the increased carbon storage, while soils were responsible for 39% of the increase. To evaluate the spatial patterns of simulated biomass change in extratropical terrestrial ecosystems from 1980 to 1995, we compared changes in vegetation carbon estimated by the TEM 5.0 simulations to analyses based on remote sensing and inventory data. The changes in vegetation carbon simulated by TEM 5.0 between 1980 and 1995 (Fig. 7a) have a similar spatial distribution in comparison with the changes estimated from the remote sensing analysis of Myneni et al. (2001; Fig. 7b), but the rate of sequestration is lower in the TEM simulations (Table 7). In Canada and Alaska, the estimate of carbon sequestration in vegetation simulated by TEM 5.0 is generally similar in magnitude, but somewhat less than estimates by analyses based on remote sensing and inventory data (compare biomass sink columns in Table 7). In the United States and northern Eurasia, the TEM 5.0 simulation and inventory-based studies both estimate carbon sequestration, but the magnitude of vegetation carbon storage simulated by TEM 5.0 is on the low end of the other estimates (Table 7). Similarly, the estimates of ecosystem carbon sequestration in vegetation and soils of forests by TEM 5.0 (Forest NCE in Table 7) are generally lower than other inventory-based estimates (Table 7).

From 1990 through 1995, the TEM 5.0 simulation indicates that extratropical terrestrial ecosystems stored 5.4 Pg C (0.90 Pg C yr^{-1}; Table 6), with 1.6 Pg C (0.27 Pg C yr^{-1}) stored in North America and 3.8 Pg C (0.63 Pg C yr^{-1}) stored in northern Eurasia. Compared to the 1980s, in which TEM 5.0 estimated that extratropical terrestrial ecosystems stored 0.55 Pg C yr^{-1} (0.24 Pg C yr^{-1} in North America and 0.31 Pg C yr^{-1} in northern Eurasia), simulated net carbon storage was enhanced during the 1990s by an additional 0.35 Pg C yr^{-1} in extratropical terrestrial ecosystems (Table 6); in the control simulation, the additional enhancement was slightly less (0.31 Pg C yr^{-1}; Table 6). The enhancement simulated by the TEM 5.0 simulation was located primarily in northern Eurasia (an additional 0.32 Pg C yr^{-1}). Of the additional carbon storage simulated by TEM 5.0 between the 1980s and 1990s, 0.08, 0.12 and 0.15 Pg C yr^{-1} are attributable to CO_2 fertilization, climate variability and change and land-use change, respectively. In the control simulation, the additional sequestration attributed to CO_2 fertilization (0.06 Pg C yr^{-1}), climate variability and change (0.10 Pg C yr^{-1}), and land-use change (0.15 Pg C yr^{-1}). Thus, between the 1980s and the 1990s the effects of climate variability and land use change on carbon storage as simulated by both versions of TEM were accelerating faster than the effects of increasing atmospheric CO_2.

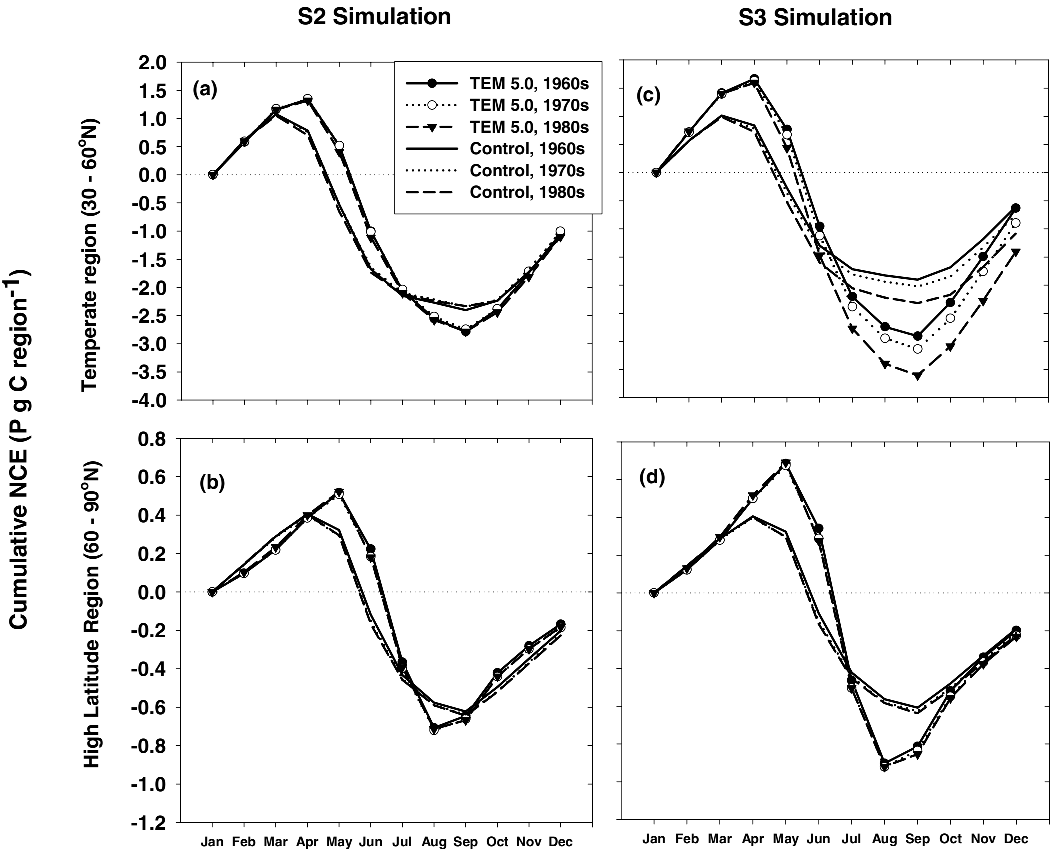

Fig. 5. The cumulative difference between NCE during the 1960s, 1970s and 1980s as estimated by the S2 simulations of TEM 5.0 and TEM 4.2 (control) for terrestrial ecosystems (a) between 30 and 60° N and (b) between 60 and 90° N; and by the S3 simulations of TEM 5.0 and TEM 4.2 for terrestrial ecosystems (c) between 30 and 60° N and (d) between 60 and 90° N. Lines with symbols indicate the results associated with soil thermal effects in TEM 5.0, and lines without symbols indicate results of the control simulation.

4. Discussion

Many large-scale biogeochemical models use monthly air temperature to drive the seasonal dynamics of NPP and R_H, and these models have been slow to incorporate the effects of soil thermal dynamics on processes that affect carbon dynamics. While it may be possible to represent how soil temperature lags air temperature in non-permafrost ecosystems, this approach is not appropriate for ecosystems affected by permafrost, as it implicitly assumes that soil thermal dynamics are determined by the movement of a single freezing front, i.e., freezing downward from the soil surface. The simulation of active layer dynamics in a permafrost-dominated system requires the consideration of two freezing fronts, i.e., freezing upward from the permafrost boundary as well as downward from the surface, as applications involving a single freezing front will generally over-predict the rate of thaw of the active layer by a factor of three in comparison to applications involving two freezing fronts (Zhuang et al., 2001; Romanovsky and Osterkamp, 1997). Also, because the response of carbon uptake by vegetation upon thaw can be characterized as an on–off switch (Frolking et al., 1999), the representation of the influence of sub-monthly freeze–thaw dynamics on carbon exchange requires a scaling approach in models that are driven by monthly temperature. In a previous study we evaluated how the incorporation of a permafrost model into a large-scale ecosystem model

Table 5. *Partitioning of net carbon exchange (as Pg C per period)*[a] *in extratropical temperate and high-latitude terrestrial ecosystems between 1920 and 1957 and 1958 and 1995 among effects attributable to changes in increasing atmospheric CO_2, climate variability and land use for both the TEM 5.0 simulation (soil thermal effects) and the TEM 4.2 simulation (control)*[b]

	1920–1957			1958–1995		
	30–60° N	60–90° N	30–90° N	30–60° N	60–90° N	30–90° N
Soil thermal effects						
CO_2	−5.9	−1.2	−7.1	−10.0	−2.1	−12.1
Climate	2.2	−0.6	1.6	−5.6	−1.5	−7.1
Land use	16.7	0.4	17.1	7.5	0.4	7.9
Sub-total	13.0	−1.4	11.6	−8.1	−3.2	−11.3
Control						
CO_2	−5.7	−1.0	−6.7	−9.5	−1.7	−11.2
Climate	3.2	−0.4	2.8	−4.6	−1.4	−6.0
Land use	16.1	0.5	16.6	7.1	0.4	7.5
Sub-total	13.6	−0.9	12.7	−7.0	−2.7	−9.7

[a]Positive values indicate net releases to the atmosphere, and negative values indicate net storage in terrestrial ecosystems.
[b]The partitioning is based on simulation S1 (CO_2), the difference of S2 and S1 (climate), and the difference of S3 and S2 (land use).

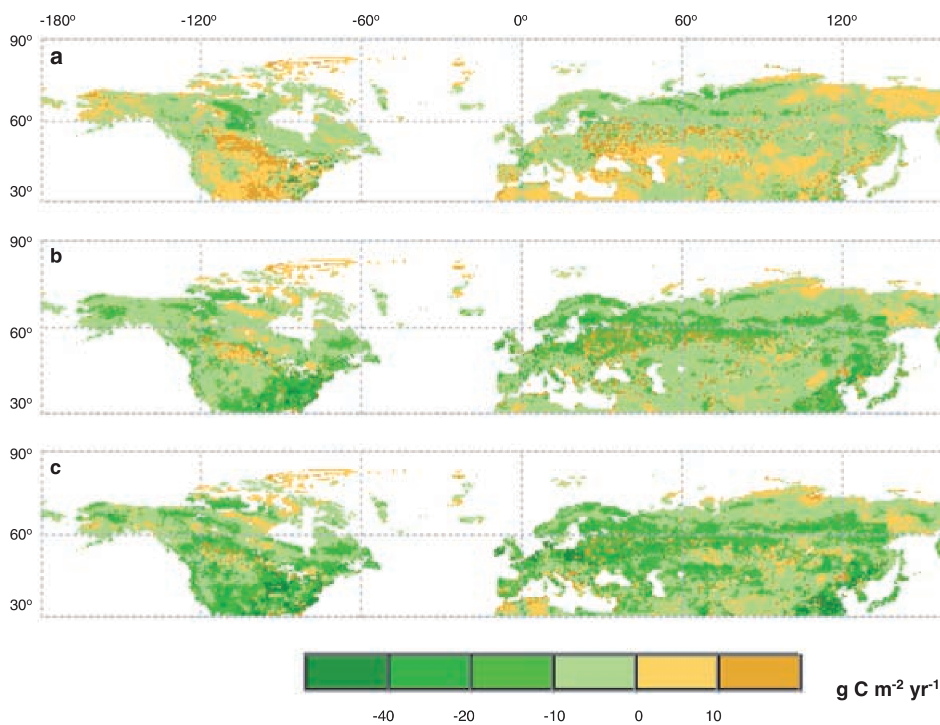

Fig. 6. The spatial distribution of NCE simulated by TEM 5.0 for the periods 1920–1957 (a), 1958–1995 (b) and 1980–1995 (c). Positive values of NCE represent sources of CO_2 to the atmosphere, while negative values represent sinks of CO_2 into terrestrial ecosystems.

Table 6. *Partitioning of net carbon exchange (as Pg C yr^{-1})*[a] *in extratropical temperate and high latitudes terrestrial ecosystems between 1980 and 1989, 1990 and 1995, and 1980 and 1995 among effects attributable to changes in increasing atmospheric CO_2, climate variability and land use for both the TEM 5.0 simulation (soil thermal effects) and the TEM 4.2 simulation (control)*

	1980–1989			1990–1995			1980–1995		
	30–60° N	60–90° N	30–90° N	30–60° N	60–90° N	30–90° N	30–60° N	60–90° N	30–90° N
Soil thermal effects									
CO_2	−0.31	−0.07	−0.38	−0.38	−0.08	−0.46	−0.34	−0.07	−0.41
Climate	−0.10	−0.02	−0.12	−0.20	−0.04	−0.24	−0.14	−0.03	−0.17
Land use	−0.05	0.00	−0.05	−0.20	0.00	−0.20	−0.10	0.00	−0.10
Sub-total	−0.46	−0.09	−0.55	−0.78	−0.12	−0.90	−0.58	−0.10	−0.68
Control									
CO_2	−0.30	−0.05	−0.35	−0.34	−0.07	−0.41	−0.31	−0.06	−0.37
Climate	−0.07	−0.03	−0.10	−0.15	−0.05	−0.20	−0.10	−0.04	−0.14
Land use	−0.05	0.00	−0.05	−0.20	0.00	−0.20	−0.10	0.00	−0.10
Sub-total	−0.42	−0.08	−0.50	−0.69	−0.12	−0.81	−0.51	−0.10	−0.61

[a]Positive values indicate net releases to the atmosphere, and negative values indicate net storage in terrestrial ecosystems.

influenced the temporal and spatial dynamics of simulated soil thermal dynamics in extratropical ecosystems (Zhuang et al., 2001). In this study we took the next logical step of scaling freeze–thaw dynamics in a large-scale ecosystem model and evaluating how the consideration of soil thermal dynamics influences the simulated dynamics of carbon exchange between extratropical terrestrial ecosystems and the atmosphere.

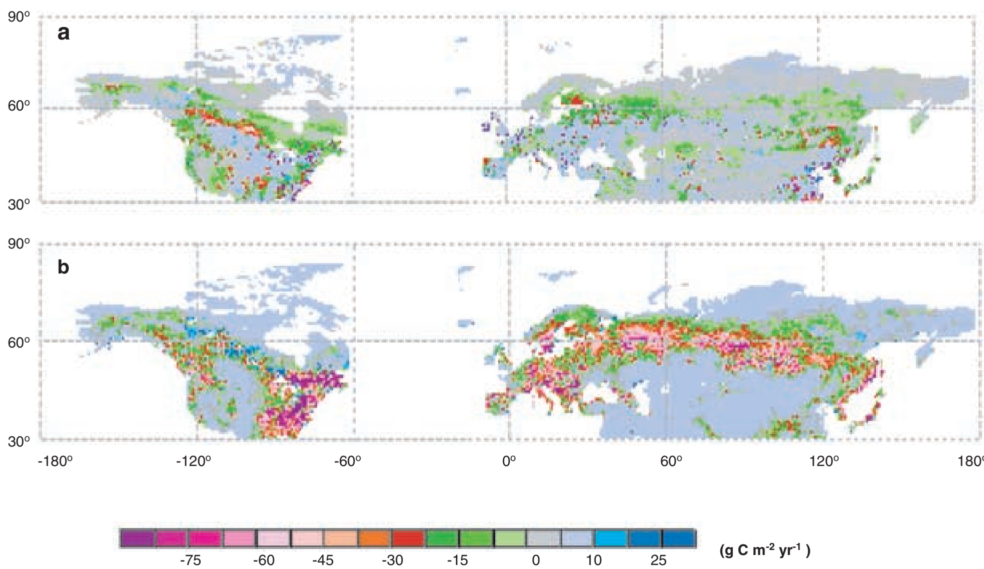

Fig. 7. A comparison of the spatial patterns of estimated annual changes in vegetation carbon storage during the 1980s and 1990s between (a) the TEM 5.0 S3 simulation and (b) the analysis of Myneni et al. (2001) based on remote sensing data. The TEM 5.0 estimates are based on differences that occurred from 1980 through 1995. The remote sensing estimates are aggregated into 0.5° × 0.5° resolution based on 0.25° × 0.25° resolution data (Myneni et al., 2001) to compare to the TEM estimates and represent differences in vegetation carbon storage between the period from 1980 to 1982 period and the period from 1995 to 1999. For easy of comparison, the color scheme used in this figure is similar to the one used in Myneni et al. (2001). Positive values in the plot represent sources of CO_2 to the atmosphere, while negative values represent sinks of CO_2 into terrestrial ecosystems.

Table 7. *Comparisons of estimates of biomass sink and forested net carbon exchange for Canada, Russia and the United States*

Country	TEM 5.0 simulation Area[a] (Mha)	TEM 5.0 simulation Biomass Sink[b] (Pg C yr^{-1})	TEM 5.0 simulation Forested NCE[b] (Pg C yr^{-1})	Inventory and other estimates Area (Mha)	Inventory and other estimates Biomass Sink[b] (Pg C yr^{-1})	Inventory and other estimates Net Change of Forest-sector Carbon Pools[b]
Canada	370.2	−0.0569	−0.0500	239.5[c]	−0.0731[c]	0.04[f]
				244.6[d]	−0.093[d]	
				404[f]	−0.085[e]	
Russia	687.4	−0.0685	−0.0790	642.2[c]	−0.2836[c]	−0.15[f]
				816.5[d]	−0.429[d]	
				763.5[g]	−0.058[g]	
				887[f]		
				770.8[h]		
United States						
Conterminous US	256.5	−0.0770	−0.0764	215.5[c]	−0.1415[c]	−0.28[f]
				217.3[d]	−0.167[d]	
				247.0[k]	−0.063[i]	
				246[f]	−0.098[j]	
					−0.020[l]	
					−0.011– −15[k]	
Alaska	65.2	−0.0039	−0.0042	52[f]		−0.0023– −0.0097[m]

[a]Forested area includes boreal forest, forested boreal wetlands, mixed temperate forests, temperate coniferous forest, temperate deciduous forest, temperate forested wetlands, temperate forested floodplains, and temperate broad-leaved evergreen forests (modified from Melillo et al., 1993).
[b]Negative values in indicate the carbon is sequestered into ecosystems.
[c]Myneni et al. (2001), Remote sensing estimates; Area is the total of forests and woodland, as defined by the distribution of broad leaf forests, needle leaf forests, mixed forests, and woody savannas (Myneni et al., 2001). Woody Biomass pool consists of wood, bark, branches, twigs, stumps, and roots of live trees, shrubs, and bushes (Myneni et al., 2001).
[d]TBFRA-2000 (Liski and Kauppi, 2000); estimates for early to mid-1990s.
[e]From inventory data (Canadian Forest Service, 1993); for 1982–1991.
[f]Goodale et al., 2002; Pool size includes above- and belowground components of trees as well as understory vegetation in 1990; the biomass sink represents the entire forest-sector balance.
[g]Nilsson et al. (2000), for 1990.
[h]Alexyev and Birdsey (1998).
[i]Turner et al. (1995); for the 1980s.
[j]Birdsey and Heath (1995); for the 1980s.
[k]Pacala et al. (2001); for 1980–1990; forest trees in coterminous United States only.
[l]Houghton et al. (1999); for the 1980s; land-use study.
[m]Yarie and Billings (2002); for recent decades; −0.0097 for climate and no fire, −0.0023 for climate and fire.

Here we discuss the implications of the results of our simulations for carbon dynamics of extratropical terrestrial ecosystems.

4.1. *Seasonal dynamics of carbon exchange*

Heimann et al. (1998), McGuire et al. (2000a) and Dargaville et al. (2002a) compared the performance of several global biogeochemical models by using monthly estimates of CO_2 exchange by the models to simulate the seasonal cycle of atmospheric CO_2 at a number of CO_2 monitoring stations located throughout the globe. In comparison to models in which NPP is prescribed by remote-sensing data, models that used prognostic algorithms for defining the seasonality of carbon uptake generally predicted the early draw-down of CO_2 during the growing season, underestimated the degree to which atmospheric CO_2 was drawn down during the growing season, and underestimated the concentrations of atmospheric CO_2 during the non-growing season. The modeling experiments of McGuire et al. (2000a) identified that the simulation of atmospheric CO_2 concentrations during the late growing season and during the non-growing season could be improved by a simple algorithm that represented the insulative effects of snowpack in global biogeochemical models.

In our study, the timing of the draw down of CO_2 at the start of the growing season and the degree of draw-down during the growing season were substantially improved by the consideration of soil thermal dynamics. Interactions between thaw dynamics and the uptake of carbon by the canopy were primarily responsible for the delay in the draw down of atmospheric CO_2. In high latitudes the delay in uptake resulted in relatively higher NPP during July and August that was responsible for the degree of draw-down in high latitudes, while the combination of relatively higher NPP and lower R_H during the growing season was primarily responsible for greater uptake in temperate latitudes. In the control version of TEM the high-latitude bias of early carbon uptake and depressed mid-summer uptake was caused by stored nitrogen in the vegetation that was used up in the production of new tissue during spring in high latitudes when air temperature and photosynthetically active radiation were favorable for photosynthesis, but when soils were frozen. The use of this nitrogen early in the growing season resulted in less nitrogen available to support production later in the growing season when temperature conditions may be more favorable for carbon uptake. The consideration of freeze–thaw dynamics in TEM 5.0 caused a delay in carbon uptake in high latitudes that allowed stored nitrogen to be available for supporting additional production during July and August. The July peak of carbon uptake simulated by TEM 5.0 in high latitudes is consistent with observations of the seasonal timing of carbon exchange in high-latitude ecosystems (Vourlitis and Oechel 1997; 1999). Heterotrophic respiration simulated by TEM 5.0 was relatively lower during the growing season in temperate latitudes because the dynamics of decomposition were driven by soil temperature instead of air temperature.

In comparison to the control version of TEM that used the simple algorithm of McGuire et al. (2000a) for considering the insulative effects of snowpack during the non-growing season, the concentrations of atmospheric CO_2 simulated by TEM 5.0 tended to be overestimated late in the non-growing season. Therefore, it is important to better understand controls over decomposition during the non-growing season and during the transition from the non-growing season to the growing season. A number of studies have examined how microbial activity is influenced by low temperature (Mazur, 1980; Coxson and Parkinson, 1987; Zimov et al., 1993; 1996; Brooks et al., 1995; 1996; 1997; Clein and Schimel, 1995), how freeze–thaw processes affect biogeochemical processes (Schimel and Clein, 1996; Oechel et al., 1997; Coyne and Kelley, 1971; Goulden et al., 1998; Eriksson et al., 2001), and how soil carbon and nitrogen dynamics interact in cold soils (Mitchell et al., 2001; Groffman et al., 2001; Fitzhugh et al., 2001). Recent evidence indicates that the nature of temperature control over heterotrophic respiration qualitatively changes across the freeze/thaw boundary (Michaelson and Ping, 2002). In future studies we need to evaluate how consideration of this new understanding influences the simulated temporal dynamics of decomposition at large spatial scales. Overall, our results indicate that an explicit consideration of soil thermal dynamics in global biogeochemical models can substantially reduce biases in the seasonal exchange of CO_2 that were identified by Heimann et al. (1998); McGuire et al. (2000a) and Dargaville et al. (2002a).

4.2. *Long term and recent changes in carbon storage*

The estimates of carbon storage simulated by TEM 5.0 and the control version of the model during the 1980s for extratropical terrestrial ecosystems (0.5–0.6 Pg C yr^{-1}) and from 1990 through 1995 (0.8–0.9 Pg C yr^{-1}) are at the low end of estimates based on atmospheric inverse models of 0.6–2.3 Pg C yr^{-1} during the 1980s and 0.7–1.8 Pg C yr^{-1} from 1990 through 1996 (Prentice et al., 2001). Similarly, the spatial patterns of carbon storage simulated by the two versions of TEM from 1990 through 1995 between North America (0.20–0.27 Pg C yr^{-1}) and northern Eurasia (0.60–0.63 Pg C yr^{-1}), are somewhat less than estimates based on atmospheric inverse models of 0.8 Pg C yr^{-1} in North America (range of 0.1 Pg C yr^{-1} loss to 2.1.Pg C yr^{-1} storage) and 1.7 Pg C yr^{-1} in northern Eurasia (0.2–2.5 Pg C yr^{-1} storage) from 1990 through 1994 (Schimel et al., 2001). The estimates of carbon sequestration in vegetation by TEM 5.0 also have similar spatial patterns in comparison to analyses based on remote sensing and inventory data, but are lower in magnitude. Thus, although the carbon sinks simulated by TEM 5.0 in the 1980s and 1990s were lower in comparison to estimates based on other methodologies, they are consistent with the decadal variability between the 1980s and 1990s and the spatial variability between North America and northern Eurasia estimated by the other methodologies. In addition, our simulations with TEM indicate that in comparison to the 1980s, sink activity during the first half of the 1990s is accelerating faster in northern Eurasia than in North America.

Several recent studies argue that the start of the growing season is occurring progressively earlier in extratropical terrestrial ecosystems over the last several decades, and that the earlier growing season is associated with climatic warming (Keeling et al., 1996; Myneni et al., 1997; Keyser et al., 2000; Zhou et al., 2001). A modeling analysis by Randerson et al. (1999) indicates that enhanced uptake of carbon by terrestrial ecosystems in the early part of the Northern Hemisphere growing season explains recent changes in seasonal cycle of atmospheric CO_2 concentrations that have been observed at some high latitude monitoring stations, i.e., an increase in the peak to peak amplitude over the annual cycle. Analyses of carbon exchange measured by eddy covariance techniques indicate that the annual net carbon uptake or loss of extratropical terrestrial ecosystems primarily depends on the timing of the start of the growing season (Frolking et al., 1996; Goulden et al., 1998; Baldocchi et al., 2001). Among eddy covariance studies in temperate broadleaf forests, the net storage of carbon increases by about 5.7 g C m^{-2} d^{-1} for each additional day that the growing season is extended (Baldocchi et al., 2001). Thus, there is an emerging body of evidence that associates trends for increased carbon storage of extratropical terrestrial ecosystems over the last several decades with an earlier growing season. Our a priori expectations were that explicit consideration of soil thermal dynamics would promote carbon storage through the effects of climate warming on the start of the growing season.

Both versions of TEM indicate that climate variability and change promoted the loss of carbon from temperate ecosystems during the first half of the 20th century, and promoted carbon storage during second half of the century. In both versions of the model, warming in the second half of the century tends to increase nitrogen availability in soils of extratropical ecosystems by enhancing decomposition (Fig. 8a). While there are differences in the depth of snow cover between the first half and the second half of the 20th century, the differences do not explain the increasing net nitrogen mineralization rates simulated in the second half of the century (Fig. 8a). The uptake of this nitrogen by the vegetation transfers nitrogen from the soil to the vegetation and allows that nitrogen to be used to enhance the uptake of carbon (McGuire et al., 1992; Melillo et al., 1993; see also Shaver et al., 1992 and Vukicevic et al., 2001). While the consideration of soil thermal dynamics consistently reduced carbon losses or enhanced carbon storage, the magnitudes of the effects were not as strong as our a priori expectations, since the simulated effect of climate change and variability on promoting the earlier uptake of carbon was very modest and occurred primarily between the 1960s and the 1970s. In contrast, our analysis indicates that land use change in the temperate zone has a strong effect in promoting earlier carbon uptake (Figs. 5 and 8b). We have identified two mechanisms by which this can occur. First, if agricultural abandonment has led to the growth of forests that store more carbon than agricultural systems throughout the growing season, then it is possible to have an earlier zero-crossing point of positive carbon gain. Second, in comparison to agricultural systems managed as summer cropping systems, native vegetation and forests begin production several weeks earlier. Thus, cropland abandonment has the potential to cause an earlier growing season because of phenological differences between agricultural systems and natural vegetation. We believe that the mechanism of the first explanation is better represented in our simulations than the mechanisms of the second explanation, as the implementation of agriculture in TEM is rather simple. Thus, our simulations may be underestimating the effects of agricultural abandonment on both changes in the seasonality and the annual magnitude of carbon uptake in recent decades if the second explanation is important.

4.3. *Summary*

Our analyses in this study indicate that soil thermal dynamics substantially influence the seasonality of carbon exchange of extratropical terrestrial ecosystems with the atmosphere through the effects of freeze–thaw dynamics on carbon uptake and decomposition. The consideration of soil thermal dynamics reduced biases in the seasonal exchange of carbon with the atmosphere that not only are found in the control version of TEM, but that also occur in other global biogeochemical models (Heimann et al., 1998; McGuire et al., 2000a; Dargaville et al., 2002b). While our study represents a major advance in representing soil thermal dynamics and terrestrial cryospheric processes in modeling the global carbon cycle, the spatial specification of lower boundary conditions for permafrost in our study did not reflect the discontinuous nature

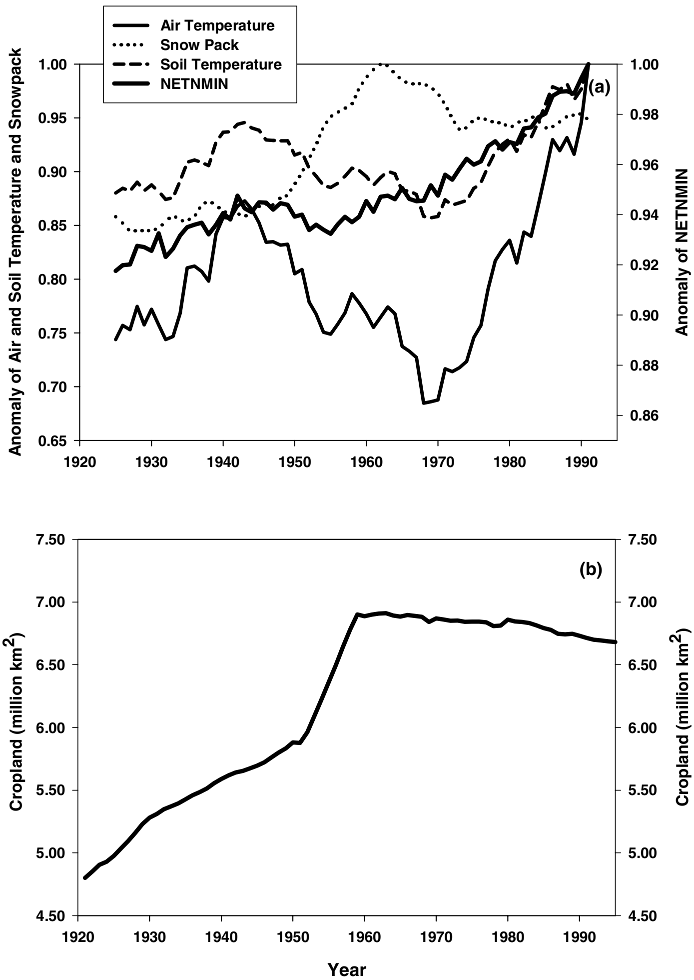

Fig. 8. Anomaly of air temperature, simulated snow pack, soil temperature and net nitrogen mineralization (NETNMIN) with TEM 5.0; the annual values were normalized to the range 0–1 and the data shown as 10 yr running mean (a) and land use (cropland) areas in extraotropics of the Northern Hemisphere from 1920 to 1995 (b).

of permafrost across the boreal forest. The development of spatially resolved data sets that describe the distribution of permafrost in extratropical ecosystems is necessary to facilitate additional progress in accurately representing the role of soil thermal dynamics and cryospheric processes in the carbon dynamics of extratropical terrestrial ecosystems.

In comparison to estimates based on inverse models and on remote sensing and inventory analyses, the simulations of carbon sequestration by TEM 5.0 are lower. This suggests that other issues besides the role of soil thermal dynamics may be responsible, in part, for the temporal and spatial dynamics of carbon storage of extratropical terrestrial ecosystems. Besides the issue of phenological differences between agricultural systems and natural vegetation, other important issues that we did not consider in this study include the role of nitrogen deposition and fire disturbance in the carbon dynamics of extratropical terrestrial ecosystems. Anthropogenic nitrogen deposition may be contributing ~0.2–0.5 Pg C yr^{-1} to carbon storage (Townsend et al., 1996; Holland et al., 1997; Nadelhoffer et al., 1999; Lloyd, 1999; Schimel et al., 1996). We are currently conducting a study with TEM 5.0 to evaluate the role of nitrogen deposition in the context of increasing atmospheric CO_2, climate, soil thermal dynamics and land use (Kicklighter et al., in preparation). Fire is an important issue that influences carbon dynamics of extratropical terrestrial ecosystems (McGuire et al., 2002a), and an inverse analysis by Dargaville et al. (2002b) suggests that fire likely plays a role in the inter-annual variability of carbon dynamics of extratropical terrestrial ecosystems at continental and sub-continental scales. Soil thermal dynamics are substantially affected by fire in permafrost dominated ecosystems because of the removal of moss and organic soil (Zhuang et al., 2002). The fire cycle has been documented to be changing in recent decades in northwest North America, where the annual area burned has doubled since 1980 compared to decades prior to 1980 (Stocks et al., 2000; Podur et al., 2002). Also, reduced fire frequency in temperate North America may be affecting carbon storage at continental scales (Houghton et al., 1999; Schimel et al., 2000). We are currently conducting a study focused on Alaska and Canada with TEM 5.0 to explicitly include fire in our modeling analyses so that we can consider interactions between the fire cycle and soil thermal dynamics in extratropical terrestrial ecosystems (McGuire et al., in preparation). In conclusion, we have made substantial progress in this study to reduce biases in the simulation of carbon dynamics of extratropical terrestrial ecosystems by explicitly considering the role of soil thermal dynamics and cryospheric processes in modeling the global carbon cycle. This progress will allow us to better consider the role of additional issues that influence carbon dynamics in terrestrial regions that experience seasonal freezing and thawing of soil.

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