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Spatially Explicit Parameterization of a Terrestrial Ecosystem Model and Its Application to the Quantification of Carbon Dynamics of Forest Ecosystems in the Conterminous United States

Min Chen*

Department of Earth & Atmospheric Sciences, Purdue University, West Lafayette, Indiana

Qianlai Zhuang

Department of Earth & Atmospheric Sciences, and Department of Agronomy, Purdue University, West Lafayette, Indiana

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ABSTRACT: The authors use a spatially explicit parameterization method and the Terrestrial Ecosystem Model (TEM) to quantify the carbon dynamics of forest ecosystems in the conterminous United States. Six key parameters that govern the rates of carbon and nitrogen dynamics in TEM are selected for calibration. Spatially explicit data for carbon and nitrogen pools and fluxes are used to calibrate the six key parameters to more adequately account for the spatial heterogeneity of ecosystems in estimating regional carbon dynamics. The authors find that a spatially explicit parameterization results in vastly different carbon exchange rates relative to a parameterization conducted for representative ecosystem sites. The new parameterization method estimates that

* Corresponding author address: Min Chen, Civil Engineering Building, 550 Stadium Mall Drive, West Lafayette, IN 47907-2051.

E-mail address: chenm@purdue.edu

the net ecosystem production (NEP), the annual gross primary production (GPP), and the net primary production (NPP) of the regional forest ecosystems are 61% (0.02 Pg C; 1 Pg = 10^{15} g) higher and 2% (0.11 Pg C) and 19% (0.45 Pg C) lower, respectively, than the values obtained using the traditional parameterization method for the period 1948–2000. The estimated vegetation carbon and soil organic carbon pool sizes are 51% (18.73 Pg C) lower and 29% (7.40 Pg C) higher. This study suggests that, to more adequately quantify regional carbon dynamics, spatial data for carbon and nitrogen pools and fluxes should be developed and used with the spatially explicit parameterization method.

KEYWORDS: Carbon dynamics; Parameterization; Spatial; United States; Forest; Terrestrial Ecosystem Model

1. Introduction

The global carbon cycle plays an important role in affecting the climate system (Cramer et al. 1999). Quantifying the dynamics of carbon exchange between the biosphere and the atmosphere is important in the understanding of global climate change. To date, many process-based biogeochemical models have been used to quantify carbon dynamics (Bonan 1995; McGuire et al. 1992; Potter et al. 1993; Running and Coughlan 1988; Zhuang et al. 2003). These models incorporate the biological, physical, and chemical processes of ecosystems and use mathematical equations to represent these processes. These mathematical equations are usually parameterized for representative vegetation types and then extrapolated to regional scales. For example, the Terrestrial Ecosystem Model (TEM) has been widely used to study ecosystem carbon and nitrogen dynamics at different scales since the early 1990s (Kicklighter et al. 1999; McGuire et al. 1992; McGuire et al. 2001; Melillo et al. 1993; Raich et al. 1991; Zhuang et al. 2002; Zhuang et al. 2003; Zhuang et al. 2006; Tang and Zhuang 2008; Tang and Zhuang 2009). In TEM, a number of parameters are used to describe and govern the physical processes of carbon, nitrogen, water, and thermal dynamics in the represented ecosystems. The parameters related to hydrologic and thermal processes are mostly determined by literature review or independent estimation using published data; however, some TEM-specific internal parameters that control the rates of carbon and nitrogen processes cannot be determined directly from the experimental measurement data but rather have to be determined through model parameterization. Traditionally, the parameterization of TEM is conducted with field data for typical ecosystem types. However, especially for the forest ecosystem, this treatment does not address the uncertainty due to the spatial heterogeneity of a region, which arises as a result of variation in stand age, species, and geographic location (Bondeau et al. 1999; Ruimy et al. 1999; Schloss et al. 1999). For instance, the aboveground productivity of forests has been reported to decrease with forest age, which may be a result of the altered carbon balance between photosynthesis and ecosystem respiration, as well as the decreased soil nutrient availability (Gower et al. 1996; Pregitzer and Euskirchen 2004; Pietsch and Hasenauer 2006). Leaf aging can also affect plant photosynthetic capacity (Kitajima et al. 1997). Bresson et al. (Bresson et al. 2009) presented evidence for altitudinal increases in photosynthetic capacity using gas exchange measurements. Turner et al. (Turner et al. 1995) reported that forests with different age classes, geographic locations, and species types had different rates of carbon fluxes and pools in the conterminous United States.

Because the rate-controlling parameters in TEM are strongly related to the rates of processes, the above evidence suggests that using a single set of parameters calibrated at representative sites for a specific broad vegetation type, but neglecting the spatial heterogeneity of the ecosystems, can result in significant uncertainty for a regional quantification.

Ideally, spatially explicit parameters for TEM are needed for regional simulations. With more available data reporting vegetation and soil carbon and nitrogen pools (Van Deusen and Heath 2010a; Van Deusen and Heath 2010b) and flux (e.g. Zhao et al. 2005), parameterization of TEM for all grid cells at a regional scale is possible. Here, we conduct a study to obtain such data and to evaluate the carbon dynamics of forest ecosystems in the conterminous United States for the period 1948–2000. We first develop spatial distributions for the key parameters of the model, TEM. Second, we evaluate the differences in carbon fluxes and pool sizes between those determined using a traditional parameterization method and those determined using the spatially explicit parameterization method. TEM is calibrated using the required spatial datasets for the forests of the conterminous United States in order to obtain the spatially explicit parameters. TEM simulations are conducted for the period 1948–2000 with both the spatially explicit parameters and the parameters obtained using the traditional method.

2. Methods

2.1. Terrestrial Ecosystem Model and its calibration

The TEM is a well-documented, process-based ecosystem model that describes the carbon and nitrogen dynamics of plants and soils in terrestrial ecosystems (McGuire et al. 1992; McGuire et al. 2001; Melillo et al. 1993; Raich et al. 1991; Zhuang et al. 2001; Zhuang et al. 2002; Zhuang et al. 2004; Zhuang et al. 2003). TEM uses spatially referenced information on climate, elevation, soils, vegetation, and water availability as well as soil- and vegetation-specific parameters to make monthly estimates of important carbon and nitrogen fluxes and pool sizes for terrestrial ecosystems.

In TEM, specific parameters control the magnitude of carbon and nitrogen fluxes (Table 1). The TEM traditional parameterization method uses carbon and nitrogen pools and annual fluxes from intensively studied sites (McGuire et al. 1992) to estimate the values for each of the rate-controlling parameters. The ecosystem data needed for a site-level calibration of TEM include 1) vegetation and soil organic carbon pool sizes (VEGC and SOLC); 2) vegetation and soil nitrogen carbon pool sizes (VEGN and SOLN); 3) gross primary production (GPP) and net primary production (NPP); 4) NPP without N limitation (NPPsat); 5) inorganic N in soil (N_{av}); and 6) N uptake of vegetation (NUPTAKE). Parameters associated with carbon and nitrogen fluxes in TEM are sequentially adjusted until all carbon and nitrogen pools, as well as annual GPP and NPP, match the observations. Here, we focus on six key parameters that are identified from our previous sensitivity study (Tang and Zhuang 2009). These parameters are C_{max} , representing the maximum photosynthesis rate; K_r and K_d , describing the rate of autotrophic and heterotrophic respiration, respectively; CFALL, indicating the carbon litterfall rate; and N_{max} and N_{up} , which are related to the N feedback for C and N uptake in vegetation. The

Table 1. Vegetation-specific parameters used in TEM. Here, C_{\max} , K_r , K_d , CFALL, N_{\max} , and N_{up} are selected as the key parameters in the spatially explicit parameterization.

Acronym	Definition	Unit
Parameters by calibration in our study		
C_{\max}	Maximum rate of photosynthesis	$\text{g m}^{-2} \text{ month}^{-1}$
K_r	Plant respiration rate at 10°C	$\text{mg m}^{-2} \text{ month}^{-1}$
K_d	Heterotrophic respiration rate at 10°C	$\text{mg m}^{-2} \text{ month}^{-1}$
CFALL	Proportion of vegetation carbon loss as litterfall monthly	$\text{g g}^{-1} \text{ month}^{-1}$
N_{\max}	Maximum rate of N uptake by vegetation	$\text{mg m}^{-2} \text{ month}^{-1}$
N_{up}	Ratio between N immobilized and C respired by heterotrophs	mg g^{-1}
Parameters by estimation from literature review or independent analysis in our study		
k_c	Half saturation constant for CO_2 -C uptake by plants	$\mu\text{L L}^{-1}$
k_i	Half saturation constant for PAR use by plants	$\text{J cm}^{-2} \text{ day}^{-1}$
T_{\min}	Minimum temperature for GPP	°C
T_{opt}	Optimum temperature for GPP	°C
T_{\max}	Maximum temperature for GPP	°C
NFALL	Proportion of vegetation nitrogen loss as litterfall monthly	$\text{g g}^{-1} \text{ month}^{-1}$
VEGC2N	Mean C:N ratio of vegetation	g g^{-1}
RAQ10A0	Leading coefficient of the Q10 model for plant respiration	None
RAQ10A1	First-order coefficient of the Q10 model for plant respiration	°C ⁻¹
RAQ10A2	Second-order coefficient of the Q10 model for plant respiration	°C ⁻²
RAQ10A3	Third-order coefficient of the Q10 model for plant respiration	°C ⁻³
k_{n1}	Half saturation constant for N uptake by plants	g m^{-3}
k_{n2}	Half saturation constant for N uptake by heterotrophic organisms	g m^{-3}
MINLEAF	Minimum photosynthetic capacity of vegetation	None
ALEAF	Coefficient to model the relative photosynthetic capacity of vegetation	None
BLEAF	Coefficient to model the relative photosynthetic capacity of vegetation	None
CLEAF	Coefficient to model the relative photosynthetic capacity of vegetation	None
MOISTOPT	Optimum soil moisture content for heterotrophic respiration	%
RHQ10	Change in heterotrophic respiration due to 10°C temperature increase	None

definition of these parameters and their associated processes are documented in Tables 1 and 2.

During model calibrations, the ecosystem data from each site are used to initialize the model, and the model is driven with climate data from the same location. Parameters are determined during the TEM calibration by repetitively adjusting parameters, running the model, and comparing the model estimates and observations. This process is completed according to the following strategy: first, we run the C cycle uncoupled from the N cycle in TEM in order to calculate productivities as if N were not limiting. Therefore, the parameters directly associated with calculating carbon fluxes and pool sizes can be determined in this step. GPP, NPP, and the maximum response of NPP to N fertilization (NPPsat) are used to constrain the maximum rate of C assimilation (C_{\max}). The parameter K_r is determined by the rate of autotrophic respiration (R_A), which is the difference of GPP and NPP. Here, K_d and CFALL are determined by SOLC and by the balance between VEGC and SOLC. Second, we run TEM, this time coupled with the N cycle to activate the C–N interactions and determine N-related parameters, which control N cycling rates and feedbacks on C cycle. The available inorganic N in soil and detritus (N_{av}) constrains the value of N_{up} ; the annual NUPTAKE and NPP determine N_{\max} .

Table 2. Key processes related to carbon dynamics in TEM.

Name	Key equations	Descriptions
Photosynthesis rate	$GPP = C_{max} f(PAR) f(T) f(Phenology) f(Foliage) f(C_a) G_v f(FT) f(NA)$	C_{max} is the maximum rate of C assimilation; $f(PAR)$ is a scalar that depends on monthly photosynthetically active radiation (PAR); $f(Phenology)$ is monthly leaf area relative to leaf area during the month of maximum leaf area; $f(T)$ is a scalar that depends on monthly air temperature; $f(C_a)$, G_v is a scalar that depends on atmospheric CO_2 concentration (C_a) and relative canopy conductance (G_v); $f(Foliage)$ is a logistic-hyperbolic function of VEGC (Zhuang et al. 2002), representing the allocation of canopy leaf biomass; $f(FT)$ is the freeze-thaw index; and $f(NA)$ is a scalar function that depends on monthly N available for incorporation into plant production of new tissue. The parameters N_{max} and N_{up} are used to estimate the rates of vegetation N uptake and N mineralization, which indirectly influence the calculations of $f(NA)$ (see the details in McGuire et al. 1992; Raich et al. 1991; Zhuang et al. 2002).
Litterfall rate	$L_C = CFALL \times VEGC$	CFALL is the proportion of vegetation carbon lost as litterfall; L_C is litterfall carbon (Raich et al. 1991).
Autotrophic respiration rate	$R_A = R_m + R_g$, $R_m = K_r(C_v) e^{(r_r)T}$	R_A is the autotrophic respiration rate, which is the sum of maintenance respiration R_m and growth respiration R_g . R_m is modeled as a function of plant biomass (C_v) and a scalar indicating the temperature (T) influence. K_r is a parameter representing the respiration rate of the vegetation per unit of biomass carbon at 0°C in grams per gram per month (Raich et al. 1991). r_r is the instantaneous rate of change in respiration (McGuire et al. 1992). R_g is estimated to be 20% of the difference between GPP and R_m (Raich et al. 1991).
Heterotrophic respiration rate	$R_H = K_d(C_s) e^{0.0693T}$ MOIST	R_H is the heterotrophic respiration rate, modeled as a function of soil C (C_s), mean temperature (T), the influence of soil moisture on decomposition (MOIST), and the gram-specific decomposition constant K_d (Raich et al. 1991).

The more specific steps of the calibration procedures are 1) set up the initial values of parameters and pool sizes (use the values from previous studies); 2) turn off nitrogen feedback effects; 3) manually adjust C_{\max} and run TEM until annual GPP matches the observed value, then manually adjust K_r and run TEM until annual NPP matches the observed value; 4) manually adjust K_d and run TEM until SOLC matches the observed value, then adjust CFALL and run TEM until VEGC matches the observed value; 5) because adjusting CFALL can change both VEGC and SOLC, do iterations of step 4 until SOLC and VEGC both match their observed values; 6) manually adjust C_{\max} and run the model until annual NPP matches NPPsat; 7) turn on nitrogen feedback effects; 8) manually adjust N_{up} until N_{av} is equal to its observed value, and adjust N_{max} until NPP and NUPTAKE are close to their observations; and 9) put the values of carbon and nitrogen pool sizes, as well as the parameter values, into the parameter table for model extrapolation. In each step, we control the differences between model estimates and observations within 1% error tolerance. These calibrated parameters are then used for extrapolation simulations. More details of the calibration and extrapolation methods can be found in Raich et al. (Raich et al. 1991) and McGuire et al. (McGuire et al. 1992).

2.2. Spatially explicit calibration for TEM

To date, the parameterization of TEM has been conducted at the site level of major representative ecosystems in order to conduct regional simulations. The parameterization and model were then extrapolated from these site-level observations onto a regional scale. To have a spatially explicit calibration for a region with TEM, here we develop an automatic calibration program for TEM. This program follows the traditional procedures of calibrating TEM but automatically adjusts the calibrating parameters to fit the model estimates with the observations. The program is designed based on the binary-search algorithm (Knuth 1997, 409–426) to accelerate the efficiency of finding the appropriate parameters. The program is used to parameterize TEM for each forest ecosystems grid cell in the conterminous United States at a $0.5^\circ \times 0.5^\circ$ resolution with available satellite products and forest and soil inventory data. The model and parameters are then extrapolated to the regional scale in order to examine how this forest carbon quantification differs from that determined using the traditional parameterization method. To obtain the spatially explicit parameters, we develop the spatial data of vegetation carbon pool sizes using the Carbon On Line Estimator (COLE) developed by the U.S. Department of Agriculture (USDA) Forest Service (Figure 1). COLE data are based on USDA Forest Service Forest Inventory and Analysis and Resource Planning Assessment data and enhanced by other ecological data. COLE provides county-level carbon storage for the forested regions of the United States using weighted analysis methods (Van Deusen and Heath 2010a; Deusen and Heath 2010b). We first obtain the county-level mean live tree carbon storage (VEGC) and soil organic carbon storage (SOLC) data for the conterminous United States. We then resample them into $0.5^\circ \times 0.5^\circ$ grid cells using the nearest-neighborhood method. Finally, we extract forest grid cells from a global vegetation map (Melillo et al. 1993). The nitrogen pool sizes (VEGN and SOLN) are then estimated by the carbon pool sizes using the C:N ratios (VEG_{cn} and SOL_{cn}) used in previous versions of TEM,

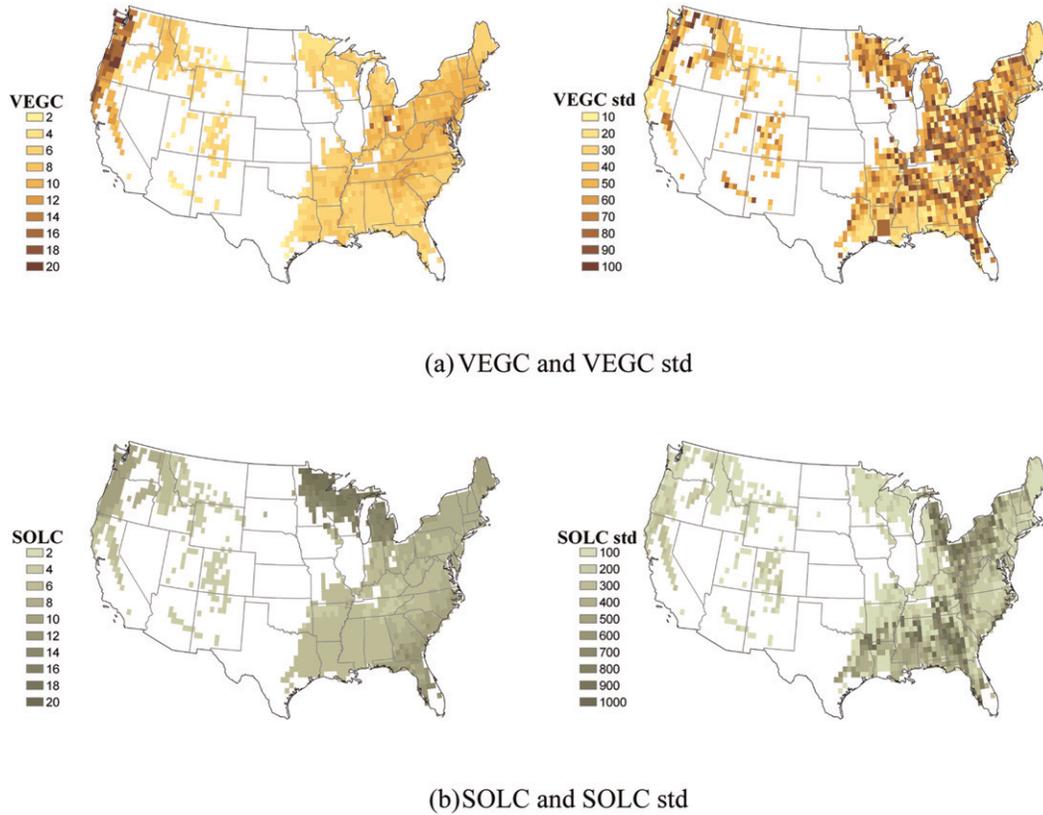


Figure 1. Spatially explicit mean carbon pool sizes and their standard errors used for calibration. Units are kg C m^{-2} and g C m^{-2} for the mean pool sizes and standard errors, respectively. (a) VEGC and VEGC std and (b) SOLC and SOLC std.

$$\text{VEGN} = \text{VEGC}/\text{VEG}_{\text{cn}} \quad \text{and} \quad (1)$$

$$\text{SOLN} = \text{SOLC}/\text{SOL}_{\text{cn}}. \quad (2)$$

Here, the VEG_{cn} and SOL_{cn} are long-term average C:N ratios. They provide an estimation of the nitrogen pool sizes for the spatially explicit parameterization and additionally provide the initial values for the C:N ratios during the parameterization procedure; these ratios will be updated for each time step for each grid cell (McGuire et al. 1992). Values of VEG_{cn} and SOL_{cn} for each ecosystem type are adapted from Zhuang et al. (Zhuang et al. 2003). The available nitrogen (N_{av}) for each ecosystem type is set as a fixed value as follows (McGuire et al. 1992): 0.5, 1.0, 2.0, and 1.5 g N m^{-2} for boreal forest, temperate coniferous forest, temperate deciduous forest, and temperate mixed forest, respectively. Additionally, in order to test the uncertainty of the model as a result of uncertain carbon pool sizes in calibration, we use the county-level standard error for carbon pool sizes from

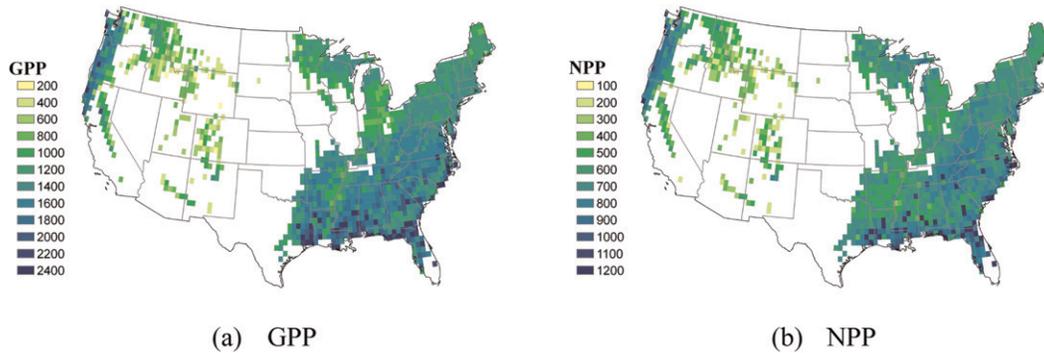


Figure 2. Annual-mean carbon fluxes for (a) GPP and (b) NPP used for calibration. Units are $\text{g C m}^{-2} \text{ yr}^{-1}$.

COLE to calibrate TEM. We resample and extract the data for forest ecosystems in the conterminous United States.

The GPP and NPP data for calibration are obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) products (Figure 2). We obtain MOD17A3_C5.1 (yearly GPP and NPP) from the Numerical Terradynamic Simulation Group (NTSG) of the University of Montana and then calculate the annual mean within the available years from 2000 to 2007. The $1 \text{ km} \times 1 \text{ km}$ pixels are then resampled into $0.5^\circ \times 0.5^\circ$ grid cells to match the spatial resolution of TEM.

The spatial values of NPP_{sat} are, however, unavailable, and we therefore estimate them using the following empirical relationship, which is suggested by (McGuire et al. 1992):

$$\text{NPP}_{\text{sat}} = 1.25\text{NPP}. \quad (3)$$

NUPTAKE is calculated as

$$\text{NUPTAKE} = \text{NPP}/\text{VEG}_{\text{cn}}. \quad (4)$$

The meteorology data used for calibration include the monthly precipitation, air temperature, and cloudiness fraction for the period 1948–2000 (Kistler et al. 2001). The 53-yr average of the meteorology data for each grid cell is used for the spatially explicit parameterization.

The Spearman’s rank correlation coefficient ρ is employed to test the spatial correlation between the calibrated parameter values and the ecosystem carbon and nitrogen pool and flux data used for calibration. The ρ indicates the direction of association between the compared variables. A positive ρ indicates the same direction as the compared variables, whereas a negative ρ indicates the opposite direction. The higher absolute value of ρ suggests a stronger correlation of the monotonic relation.

2.3. Regional simulation

To quantify carbon fluxes over the forested area of the conterminous United States and compare the differences between two simulations, one using the spatially

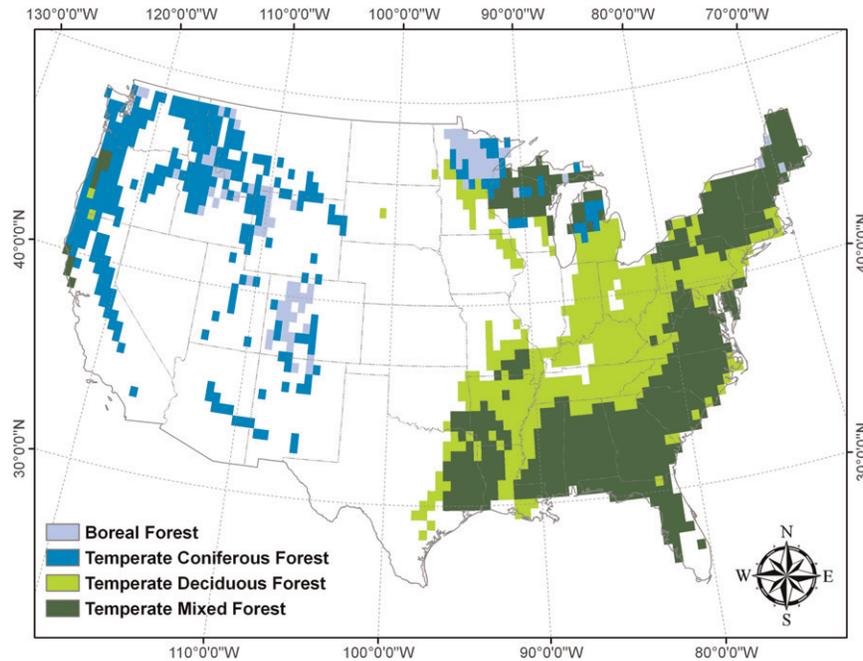


Figure 3. Potential vegetation coverage of the forest regions in the conterminous United States at a resolution of $0.5^\circ \times 0.5^\circ$ (longitude \times latitude).

explicit parameterization method and the other the traditional method, we apply TEM to the region at a $0.5^\circ \times 0.5^\circ$ spatial resolution for the period 1948–2000, for a total of 1370 grid cells (Figure 3). The spatially explicit soil texture data describing the percentage of sand, silt, and clay in the soil are originally from the published soil map of Food and Agriculture Organization of the United Nations (FAO 2011); Other auxiliary data, such as elevation, are from our previous studies (Zhuang et al. 2003). The annual atmospheric CO_2 concentration data from 1948 to 2000 are also based on data from our previous studies (Zhuang et al. 2003). We first run TEM to equilibrium and then spin up the model for 1000 years to account for the influence of climate interannual variability on the initial conditions of the ecosystems. After that, we run the model with transient climate and annual atmospheric CO_2 concentrations from 1948 to 2000.

The COLE data are supposed to be unbiased, but statistical standard errors exist in association with the mean values (Van Deusen and Heath 2010a; Van Deusen and Heath 2010b). To quantify the possible uncertainty induced by the statistical errors, we conduct ensemble calibrations using the mean carbon pool sizes and their corresponding standard errors. Because we use two carbon pools (the vegetation carbon and soil organic carbon), besides the calibration using mean values of VEGC and SOLC from COLE, four additional sets of calibrations are conducted based on the combinations of mean values (e.g., $\text{VEGC}_{\text{mean}}$ and $\text{SOLC}_{\text{mean}}$) and standard errors (e.g., VEGC_{std} and SOLC_{std}) of VEGC and SOLC, which are $\text{VEGC}_{\text{mean}} + \text{VEGC}_{\text{std}}$ and $\text{SOLC}_{\text{mean}} + \text{SOLC}_{\text{std}}$, $\text{VEGC}_{\text{mean}} + \text{VEGC}_{\text{std}}$ and $\text{SOLC}_{\text{mean}} - \text{SOLC}_{\text{std}}$, $\text{VEGC}_{\text{mean}} - \text{VEGC}_{\text{std}}$ and $\text{SOLC}_{\text{mean}} + \text{SOLC}_{\text{std}}$, and

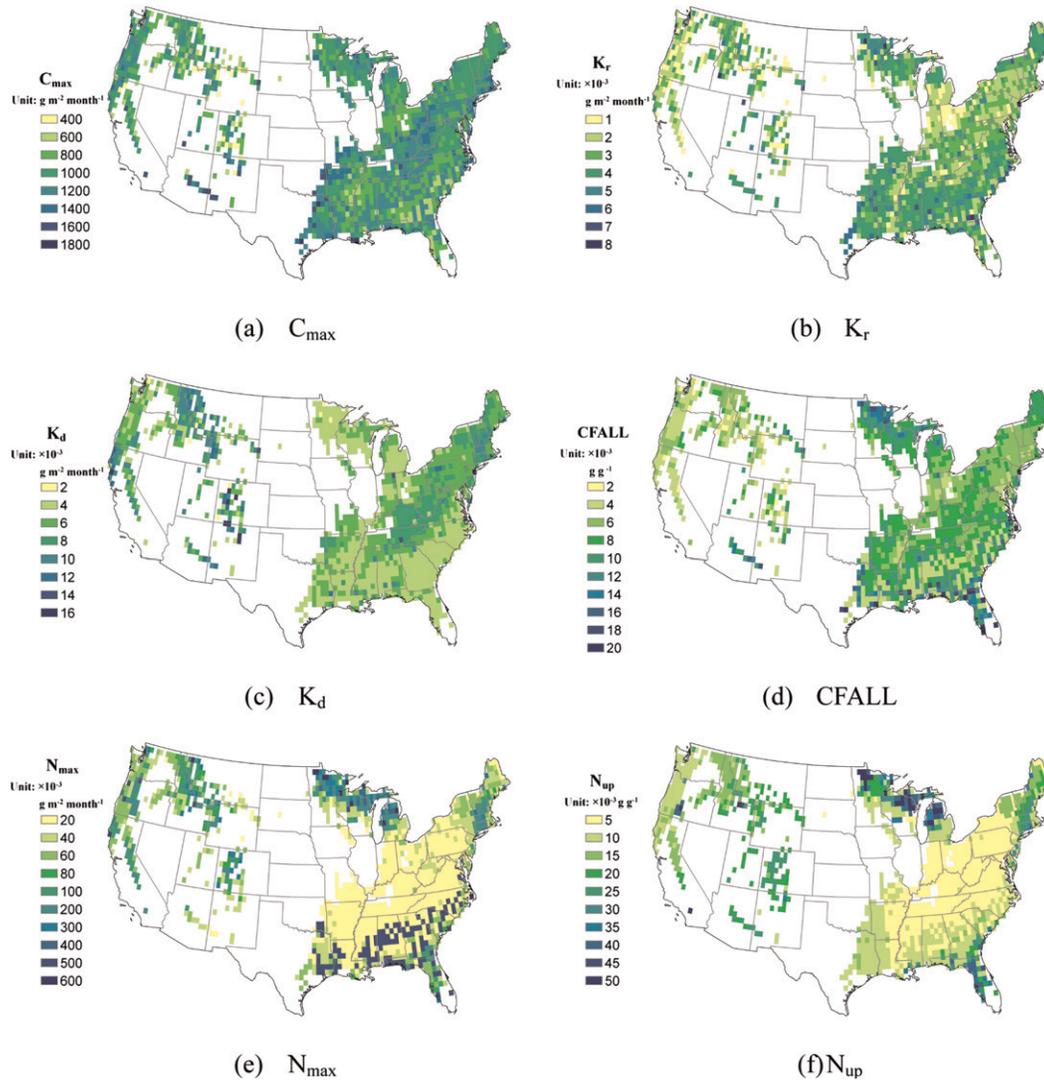


Figure 4. Spatial patterns of the calibrated key parameters: (a) C_{max} ; (b) K_r ; (c) K_d ; (d) CFALL; (e) N_{max} ; and (f) N_{up} .

$VEGC_{mean} - VEGC_{std}$ and $SOLC_{mean} - SOLC_{std}$. We then extrapolate the five sets of spatially explicit parameters to the region. Standard errors for these five sets of calibrated parameters and simulation results are used for uncertainty analysis.

3. Results

3.1. Spatial patterns of the calibrated key parameters

Parameter values vary significantly in the region (Figure 4). The highest C_{max} values are mainly observed along the Appalachian Mountains, the coastal plain, the Ozark plateaus, and the Ouachita Mountains, as well as the Pacific coastal regions.

Table 3. Spatial correlations between the spatially explicitly calibrated parameters and the variables used for calibration. Here, T stands for air temperature and P stands for precipitation.

	GPP	NPP	VEGC	SOLC	T	P
C_{\max}	0.46*	0.35*	0.02	0.004	0.16*	0.04
K_r	0.39*	0.002	-0.43*	-0.04	0.16*	0.13*
K_d	-0.07*	0.06*	0.24*	-0.39*	-0.31*	-0.29*
CFALL	0.21*	0.32*	-0.47*	0.21*	0.15*	0.15*
N_{\max}	-0.11*	0.01	-0.19*	0.24*	-0.25*	-0.35*
N_{up}	-0.31*	-0.24*	-0.39*	0.14*	-0.39*	-0.58*

* The p value for testing the hypothesis of no correlation against the alternative that there is a nonzero correlation is less than 0.05.

The spatial pattern of K_r is similar to that of C_{\max} , except for the low values in the Pacific coastal region and the high values in northern Michigan. High K_d , however, is mostly distributed in the Appalachian Mountains area, the Rocky Mountains area, and the California Coast Range area. High CFALL is mostly located in the eastern United States and especially along the Gulf Coast and the northern central plain areas. The N-related parameters have similar spatial patterns: both of which are high in the coastal plains, the northern central lowlands, the Rocky Mountains, and the Pacific coastal regions and low in the east-central United States.

The calibrated parameters are spatially associated with the input variables (Table 3). The C_{\max} is strongly and positively correlated with the GPP and NPP because it directly affects the carbon assimilation rate; the K_r is positively related to the rate of plant maintenance respiration, a portion of GPP in TEM; thus, it is significantly and positively correlated to the GPP. The K_r also has notably negative correlations with the VEGC in our simulation because respiration directly reduces the vegetation carbon pool size. For a similar reason, CFALL is positively correlated to SOLC but varies inversely with VEGC, as we would expect. The K_d indicates the rate of heterotrophic respiration, which can reduce the SOLC size. Our results show K_d varies inversely compared to the SOLC, as expected. The K_d is also found to be negatively related to air temperature and precipitation, but most likely K_d has the same direction of spatial variation as VEGC. The spatial variations of the N-related parameters (N_{\max} and N_{up}) are positively correlated with the variations in NPP.

3.2. Simulated carbon dynamics with the traditional and spatially explicit parameterization methods

The traditional parameterization estimates that the region was a C sink of 0.03 ± 0.14 Pg C yr⁻¹ with an annual GPP of 4.55 ± 0.24 Pg C yr⁻¹ and NPP of 2.37 ± 0.19 Pg C yr⁻¹ for the period from 1948 to 2000 over the total vegetated area of 3.26×10^6 km² (Table 4). The R_A and R_H for this period are 2.17 ± 0.06 and 2.34 ± 0.09 Pg C yr⁻¹, respectively. During this period, climate factors fluctuated frequently and resulted in a significant interannual variability in these carbon fluxes (Figure 5).

Overall, TEM with the spatial parameterization provides similar temporal trends for C dynamics, but with different magnitudes in comparison with the estimates from the traditional parameterization method (Figure 5). With the spatially explicit

Table 4. TEM-estimated average carbon fluxes and pool sizes over the period of 1948–2000 with the traditional and spatially explicit parameterization methods. Here, *t* stands for estimations by TEM with the traditional parameterization method; *p* stands for estimations by TEM with the spatially explicit parameterization method; and %diff = $(p - t)/t \times 100\%$ indicates the difference between the two estimations. Units are Pg C yr⁻¹.

	<i>t</i>	<i>p</i>	%diff
GPP	4.55 ± 0.24	4.46 ± 0.28	-2
NPP	2.37 ± 0.19	1.92 ± 0.19	-19
NEP	0.03 ± 0.14	0.05 ± 0.16	61
<i>R_A</i>	2.17 ± 0.06	2.54 ± 0.11	17
<i>R_H</i>	2.34 ± 0.09	1.87 ± 0.09	-20
VEGC	56.31 ± 0.68	27.58 ± 0.79	-51
SOC	25.81 ± 0.42	33.21 ± 0.25	29

parameterization, TEM estimates that the regional GPP was 4.46 ± 0.28 Pg C yr⁻¹ for the period 1948–2000, which is slightly lower than the estimates from the traditional parameterization method. The NPP and net ecosystem production (NEP) are, however, estimated to be 1.92 ± 0.19 and 0.05 ± 0.16 Pg C yr⁻¹ for the period from 1948 to 2000, which is 19.1% lower and 61% higher than the estimates from the traditional parameterization (Table 4).

The average spatial patterns of the simulated NEP by the spatially explicitly and traditionally parameterized TEM are different over the period 1948–2000 (Figures 6a,b). With the traditional parameterization, TEM-estimated carbon sinks are generally larger in the Southeast United States but smaller in the Pacific Northwest area and the central lowland area in northern Minnesota and Michigan, compared to the estimates by the spatially explicitly parameterized TEM. The carbon-source areas are also estimated to be larger in Minnesota by the traditionally parameterized TEM.

Spatial patterns and magnitudes for vegetation and soil organic carbon storage are very different with the two methods of parameterization. Kolmogorov–Smirnov tests (Corder and Foreman 2009) on the estimated carbon pool datasets from the two methods confirm that they have significant differences, rejecting the null hypothesis at the 5% significance level, with $p < 10^{-10}$ for soil organic carbon pools and $p < 10^{-100}$ for vegetation carbon pools during the study period.

A single set of parameters for each ecosystem type (the traditional parameterization method) produces more continuously homogeneous spatial patterns for the carbon pools, whereas the spatially explicit method generates more discrete spatial distributions. Both the vegetation carbon and soil organic carbon pools (Figures 6d,f) have spatial patterns similar to the initial carbon pools used for the spatially explicit parameterization. For example, the traditional method estimates the deciduous forests in the middle United States stored more vegetation carbon than the other areas, whereas the results from the spatial parameterization indicate the highest vegetation carbon storage was located in the Pacific Northwest and along the Appalachian Mountains (Figure 6c). The spatial features of the soil organic carbon estimated by the two parameterization methods are more similar to each other when comparing the differences between the vegetation carbon pools. Both predict a large amount of soil organic carbon stored in the northeastern, southeastern,

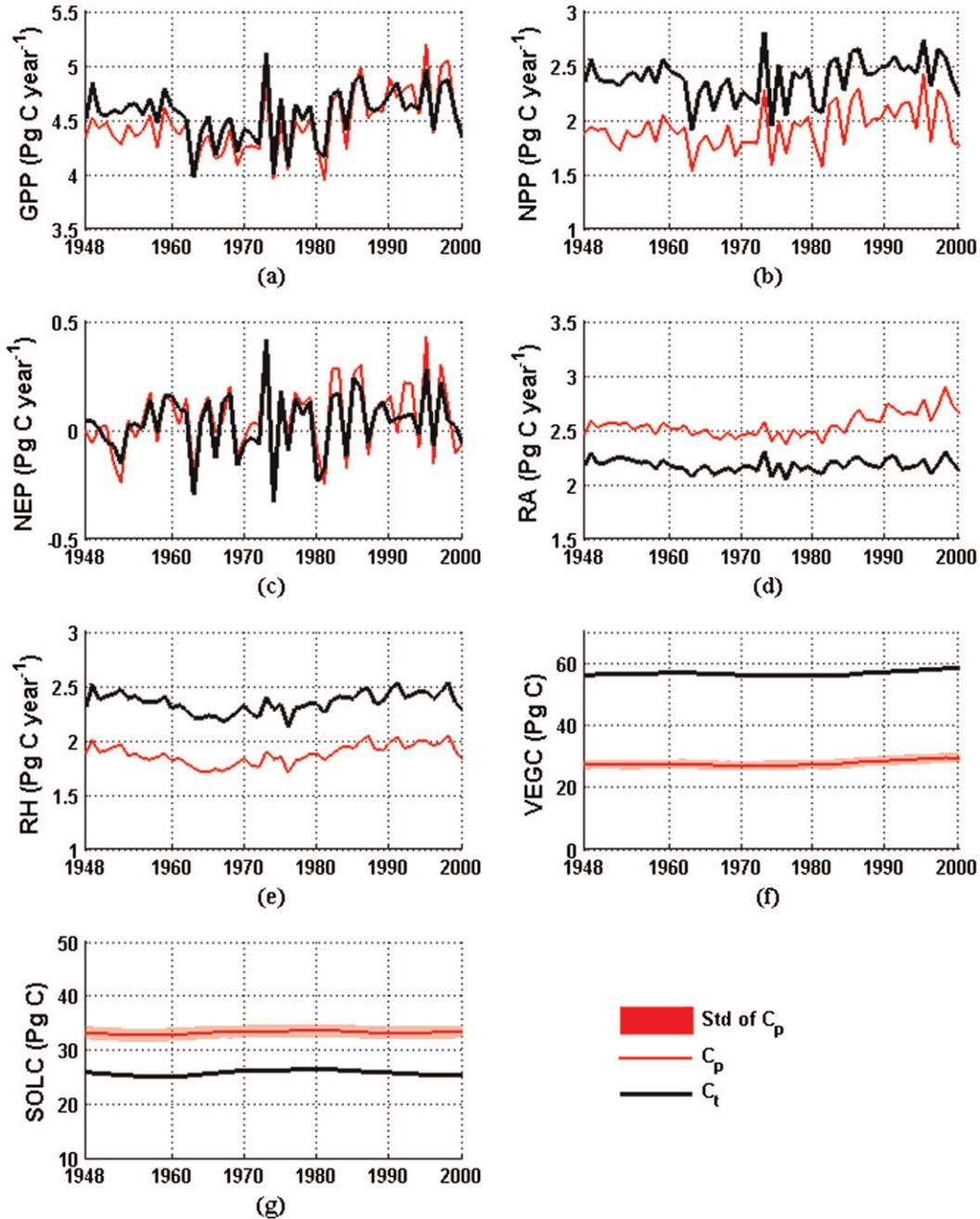


Figure 5. Annual carbon fluxes and carbon pool sizes from 1948 to 2000 of the forest ecosystems of the conterminous United States. Variations of (a) GPP, (b) NPP, (c) NEP, (d) R_A , (e) R_H , (f) VEGC, and (g) SOLC. The variable C in the legend stands for each carbon flux and pool size. The subscript p stands for using the spatial calibration method, whereas t stands for the traditional method. Here, std indicates the standard deviation of the ensemble simulation results. Note that the std is too small to be seen in (a)–(e).

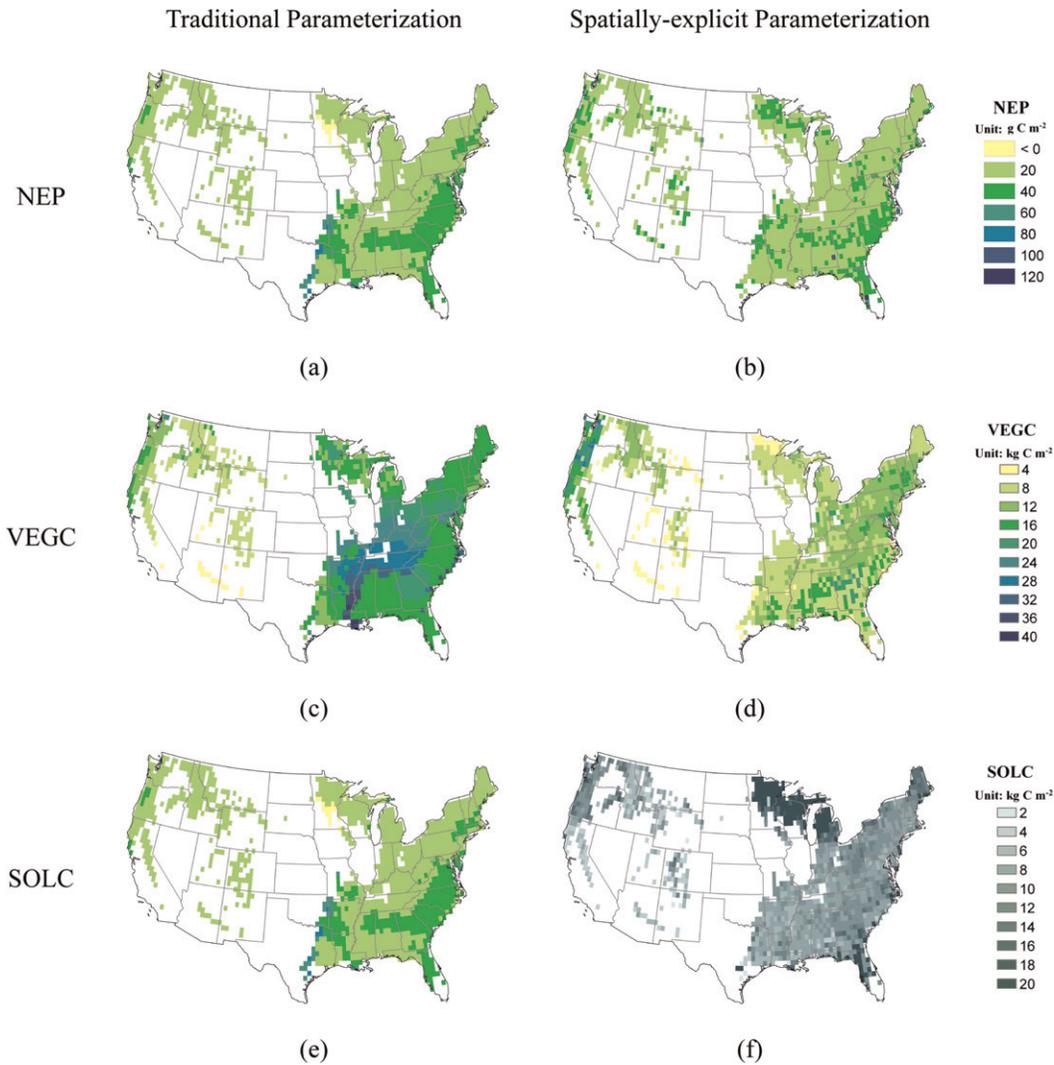


Figure 6. Spatial patterns of NEP, VEGC, and SOLC estimated using TEM with the traditional and spatially explicit parameterization methods during the period of 1948–2000. (a) NEP estimated with traditional parameterization, (b) NEP estimated with spatially explicit parameterization, (c) VEGC estimated with traditional parameterization, (d) VEGC estimated with spatially explicit parameterization, (e) SOLC estimated with traditional parameterization, and (f) SOLC estimated with spatially explicit parameterization.

and midwestern forests, although the spatial parameterization method provides higher magnitudes (Figure 6e).

4. Discussion

With the developed spatially explicit parameterization method and simulations, we must further consider four issues. One is the verification of our results for

carbon dynamics with the study region. A second focuses on investigating the role of carbon pools and fluxes in quantifying carbon dynamics. A third issue is the role of spatially explicit parameterization in regional carbon quantification. Finally, we consider the possible uncertainties associated with the use of the spatially explicit parameterization method and also future work.

4.1. Verification of the estimated carbon dynamics

There are various independently estimated carbon dynamics for the forests of the conterminous United States. Houghton et al. (Houghton et al. 1999) estimated the carbon sink in the forest of the conterminous United States to be $0.06 \text{ Pg C yr}^{-1}$ in the 1980s (Houghton et al. 1999; Pacala et al. 2001); Birdsey and Heath (Birdsey and Heath 1995) reported the carbon sink of the forested regions to be about $0.10 \text{ Pg C yr}^{-1}$ for the same period (Birdsey and Heath 1995) without considering land-use changes. However, a later study demonstrated the land-use changes have significant effects on the carbon budgets (Birdsey et al. 2006). Pacala et al. (Pacala et al. 2001) estimated the sink to be $0.11\text{--}0.15 \text{ Pg C yr}^{-1}$ for the 1980s (Pacala et al. 2001). The historical simulated results of our study suggested that the carbon sink is $0.07 \text{ Pg C yr}^{-1}$ for the 1980s with the spatially explicit parameterization method, which is closer to these independent estimations, compared with the $0.04 \text{ Pg C yr}^{-1}$ estimated by the traditional parameterization method. Zhang et al. (Zhang et al. 2010) showed that the annual NPP of the forests in the conterminous United States increased from 1.5 Pg C yr^{-1} in the early twentieth century to 1.9 Pg C yr^{-1} in the early twenty-first century (Zhang et al. 2010). NPP estimated by the spatially explicitly parameterized TEM is about $1.92 \text{ Pg C yr}^{-1}$ in the period of 1948–2000, which is lower than the traditional-method-estimated value of $2.37 \text{ Pg C yr}^{-1}$ but closer to Zhang et al.'s (Zhang et al. 2010) result. The MODIS products start in the year 2000 and, for the period of 2000–07, the MODIS products estimate the average annual GPP and NPP of the study region to be 3.98 and $1.94 \text{ Pg C yr}^{-1}$, respectively, which is closer to our estimates of the twentieth century with the spatially explicit parameterization method. Existing soil organic carbon is estimated to be about 25 Pg C (U.S. Department of Agriculture 2011), which is in between the estimations from the two methods used in our study (Table 4); however, our estimations of vegetation carbon (Table 4) with the spatially explicit parameterization is much closer to 24 Pg C (Sundquist et al. 2009). In summary, the spatially explicit parameterized TEM results presented here are broadly consistent with a wide range of previous studies on carbon dynamics in the same region.

4.2. The role of carbon pool sizes and carbon fluxes in parameterization

Estimates of the amount of carbon storage are important because they are a baseline for assessing potential future carbon storage gains or losses (Sundquist et al. 2009) and affect the net exchange of CO_2 between forests and the atmosphere (Pregitzer and Euskirchen 2004). Conceptually, the vegetation carbon pool size determines the vegetation biomass and the leaf biomass and therefore influences the photosynthesis rate as modeled in the GPP formulation in TEM (Table 2;

Zhuang et al. 2002) and the autotrophic respiration rate; the soil organic carbon pool size is also significant in the determination of heterotrophic respiration (Table 2). The nitrogen pool sizes (derived from carbon pool sizes in our study) concern the carbon–nitrogen interaction processes and therefore also play an important role in carbon dynamics. The carbon fluxes (annual GPP and NPP) used for parameterization are also of significant importance because they directly reflect the features of the ecosystem carbon assimilation rate and the autotrophic respiration rate. Technically, the related parameters are sequentially adjusted during the parameterization process in order to reach the observed carbon pool sizes and fluxes. The spatially explicit carbon pools and fluxes affect the parameter values and therefore affect spatial patterns and the magnitudes of the simulated carbon dynamics at the regional scale. As shown in our results, TEM, using the traditional parameterization, will predict much higher vegetation carbon storage in comparison with other estimates.

4.3. Importance of using spatially explicit parameters

Quantification of ecosystem carbon dynamics with TEM is influenced by parameters. Traditionally, these parameters are determined by calibrating the model at a number of representative sites. When these parameters are applied to the region, the regional grid cells are therefore assumed to have the same characteristics as the calibration sites. However, ecosystem processes are related not only to ecosystem type but also to various environmental and ecological factors (e.g., stand age, species, and geographic location) (Ahl et al. 2004; Monsi and Saeki 2005; Still et al. 2004; Turner et al. 1995). Therefore, because the model with the traditional parameterization is not able to account for the spatially heterogeneous features of the ecosystems, its estimation may be biased. The parameters for each grid cell of a region are therefore needed to better quantify the regional carbon dynamics.

To date, several studies revealed the importance of spatial parameters in model simulations. For example, De Kauwe et al. (De Kauwe et al. 2008) assimilated the spatial leaf area index (LAI) from MODIS over a coniferous forest site in Oregon into an ecosystem model with an ensemble Kalman filter, showing that assimilating the LAI data improved the NEP estimates. Studies on satellite-based terrestrial production models also suggest that the key parameter, light-use efficiency at the canopy level, varies spatially with different vegetation species, stand age, soil fertility, and climate (McCallum et al. 2009). In contrast, Davi et al. (Davi et al. 2006) tested the sensitivity of a combination of six key parameters: the above-ground wood biomass (B), the soil water reserve (SWR), the canopy clumping factor (CF), the LAI (L), the leaf mass per area of sunlit leaves (M_{sun}), and the leaf nitrogen content (N) with the process-based model CASTANEA. The study suggested a slight difference in the estimation of carbon fluxes and almost no difference in the estimation of water fluxes between using spatially explicit parameters and aggregated parameters from a small study region. Our results, however, suggest there are significantly different magnitudes and spatial patterns (e.g., Figure 6 and Table 4) for carbon dynamics in the forest ecosystems of the United States, for both the past and future, between the estimations determined using the spatially explicit and the traditional parameterization methods. Because we use the same climate forcing data and spatial reference data for the model simulations for the

two parameterization methods, the reason for the differences is most likely due to the use of the spatially explicit parameters versus the traditionally calibrated parameters. This suggests that the spatially explicit parameters are important to better quantifying regional ecosystem carbon dynamics.

4.4. Possible uncertainties and the future work

There are various possible uncertainty sources in our estimations of carbon dynamics with the spatially explicitly parameterized TEM. First, the uncertainty of the carbon pool size data used for the spatially explicit parameterization may contribute to the total uncertainty. The COLE data are based on forest inventory data and mapped with weighted analysis and have been suggested as an unbiased estimator of carbon mapping. The COLE-estimated carbon data are validated, but with statistical errors. The ensemble parameterizations are conducted to test how the errors of the carbon pool sizes affect the results. As shown in Figure 5, the standard deviation of the results of the ensemble simulations are within very small ranges, indicating that the carbon pool size error slightly alters the model estimates of carbon fluxes but notably influence the estimates of vegetation and soil organic carbon pool sizes (Figure 5). The uncertainty of the vegetation and soil organic carbon pool size estimation induced by the error in the carbon pool size in calibration is as low as about 3%–5% of the mean estimation. We also use two other types of resampling methods (bilinear and cubic) to assess the uncertainties introduced by the methods used to resample the spatially explicit carbon pools. We find the resampled results by the two methods to be similar to the results produced by the nearest-neighborhood method we used in this study. The discrepancies in both methods are in the $\pm 5\%$ tolerance range of our parameterization procedure, and therefore the uncertainties may not be obvious. The method of estimating NPP_{sat} [Equation (3)] may also contribute to the uncertainty of the model calibration and therefore estimations of carbon dynamics. During the processes of calibration, over- or underestimation of NPP_{sat} will lead to higher or lower values of C_{\max} (see the description of calibration procedures); the N limitation effect is therefore over- or underestimated in association with higher or lower N_{\max} values. LeBauer and Treseder (LeBauer and Treseder 2008) reported the ratio of estimated aboveground net primary productivity in the fertilized plots to the control plots for all biome types to be 1.22–1.35, and for temperate forests the ratio was 1.11–1.28, with a meta analysis of 126 nitrogen addition experiments evaluating the N limitation of NPP in terrestrial ecosystems. The ratio was, however, suggested to vary with geographic location and environmental conditions. The number we used in this study is within a reasonable range, but the number does not account for the spatial variability of the ratio. Further study in the future will be needed on this point. Another uncertainty may come from the nitrogen pool size. Because of data limitation, we estimate nitrogen pools using the C:N ratios of soils and vegetation in this study. Previous studies suggest that the C:N ratios may vary spatially (White et al. 2000), but recent sensitivity analysis on TEM parameters suggests TEM is not sensitive to the values of the initial C:N ratios as parameters (Tang and Zhuang 2009). Future effort should be made to provide more accurate spatially explicit pool sizes for nitrogen in both vegetation and soils to better quantify regional carbon dynamics.

In addition, GPP and NPP are directly correlated to the photosynthesis rate; thus, the errors in the GPP and NPP spatial data will result in a bias in the estimation of C_{\max} (i.e., a higher GPP and NPP will have a higher C_{\max}). Moreover, the gap between GPP and NPP is controlled by the parameter K_r , and thus an overestimation of the gap will lead to an overestimation of K_r and vice versa. Here, we use the spatial data from the MODIS GPP and NPP product, which were generated with a combination of satellite observations and process-based models (Running et al. 2004; Zhao et al. 2005). Although the satellite products were well validated with eddy flux tower data (Heinsch et al. 2006; Plummer 2006; Turner et al. 2006; Zhao et al. 2006), it might be more proper to use independent satellite-based estimations in the future (e.g. Xiao et al. 2008; Xiao et al. 2010; Yang et al. 2007). For future studies at a larger regional scale, several soil carbon inventory databases are available (Fischer et al. 2008; U.S. Department of Agriculture 2011). However, the spatial distribution of vegetation carbon storage for the conterminous United States or the globe is not available. With the development of lidar and radar remote sensing (Dubayah and Drake 2000; Kobayashi et al. 2000; Lefsky et al. 2009; Yu et al. 2010), it is possible to gradually get a global estimation of vegetation carbon pool sizes, which could be directly used as an input for the spatially explicit parameterization of TEM for a better quantification of ecosystem dynamics at regional and global scales.

Finally, the vegetation map we used in the spatially explicit calibration and the base land-cover map from the MODIS carbon flux products are not exactly matched with one another. The COLE data do not have a base land-cover map but are based on the county level. The potential vegetation map used in this study from Mellilo et al. (Mellilo et al. 1993) is at a $0.5^\circ \times 0.5^\circ$ resolution. At the $1 \text{ km} \times 1 \text{ km}$ level, both of these maps are coarser than the MODIS products. Errors therefore occur as a result of rescaling and matching these data onto the same spatial scale and range. In addition, these maps are produced in different periods, during which land-use and land-cover change may have happened. Therefore, mismatch of the vegetation maps of these data could happen, and it may affect the parameterization results and the model extrapolation results, mainly due to the following two reasons: 1) mistake in a grid's vegetation type will result in the usage of improper parameters (e.g., VEG_{cn} , Nav) during the spatially explicit calibration and thus produce wrong calibrations and 2) because the MODIS GPP and NPP products are based on MODIS land-cover products, the MODIS product may provide improper GPP and NPP data for a grid cell because of the mismatch of the MODIS land cover and the vegetation-cover type in this study. As discussed above, the errors in GPP and NPP may bring uncertainty to the results. In the current study, we rescaled all of the data into $0.5^\circ \times 0.5^\circ$ grid cells because of the limit of computing resources and the consideration of the coarse COLE data, but a future study may conduct the spatially explicit parameterization at a higher spatial resolution and based on a unifying land-cover map to reduce the uncertainty.

5. Summary

Our study uses a spatially explicit parameterization method in our process-based ecosystem model. The new parameterization method is able to more adequately deal with the spatial heterogeneity of the ecosystems for the conterminous United

States in estimating the carbon dynamics of forest ecosystems. The model parameters have high spatial variation in concert with highly heterogeneous soil and vegetation carbon distributions. The spatially explicit parameters, therefore, lead to distinct estimates of carbon dynamics of the conterminous United States forest ecosystems compared with the results from a traditional parameterization method. With the new parameterization method, the model estimates the net carbon exchanges between the conterminous United States forest ecosystem and the atmosphere to be 61% higher than the value estimated by the traditional method during the period of 1948–2000. The large difference between the two regional estimates indicates the importance of the spatially explicit parameters. This study suggests that more spatially explicit vegetation and soil carbon, nitrogen, and flux data are needed and should be used to improve future quantification of carbon dynamics at regional and global scales.

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