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A. David McGuire; Jerry M. Melillo; David W. Kicklighter; Linda A. Joyce

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Equilibrium responses of soil carbon to climate change: empirical and process-based estimates

A. DAVID MCGUIRE, JERRY M. MELILLO, DAVID W. KICKLIGHTER and LINDA A. JOYCE* *The Ecosystems Center, Marine Biological Laboratory, Woods Hole MA 02543, U.S.A and *Rocky Mountain Forest and Range Experiment Station, USDA Forest Service, Fort Collins, CO, 80526, U.S.A.*

Abstract. We use a new version of the Terrestrial Ecosystem Model (TEM), which has been parameterized to control for reactive soil organic carbon (SOC) across climatic gradients, to evaluate the sensitivity of SOC to a 1°C warming in both empirical and process-based analyses. In the empirical analyses we use the steady state SOC estimates of TEM to derive SOC-response equations that depend on temperature and volumetric soil moisture, and extrapolate them across the terrestrial biosphere at 0.5° spatial resolution. For contemporary climate and atmospheric CO₂, mean annual temperature explains 34.8% of the variance in the natural logarithm of TEM-estimated SOC. Because the inclusion of mean annual volumetric soil moisture in the regression explains an additional 19.6%, a soil moisture term in an equation of SOC response should improve estimates. For a 1°C warming, the globally derived empirical model estimates a terrestrial SOC loss of 22.6 10¹⁵ g (Pg), with 77.9% of the loss in extra-tropical ecosystems. To explore whether loss estimates of SOC are affected by the spatial scale at which the response equations are derived, we derive equations for each of the eighteen ecosystems considered in this study. The sensitivity of terrestrial SOC estimated by summing the losses predicted by each of

the ecosystem empirical models is greater (27.9 Pg per °C) than that estimated by the global empirical model; the 12.2 Pg loss (43.7%) in tropical ecosystems suggests that they may be more sensitive to warming. The global process-based loss of SOC estimated by TEM in response to a 1°C warming (26.3 Pg) is similar to the sum of the ecosystem empirical losses, but the 13.6 Pg loss (51.7%) in extra-tropical ecosystems suggests that they may be slightly less sensitive to warming. For the modelling of SOC responses, these results suggest that soil moisture is useful to incorporate in empirical models of SOC response and that globally derived empirical models may conceal regional sensitivity of SOC to warming. The analyses in this study suggest that the maximum loss of SOC to the atmosphere per °C warming is less than 2% of the terrestrial soil carbon inventory. Because the NPP response to elevated CO₂ has the potential to compensate for this loss, the scenario of warming enhancing soil carbon loss to further enhance warming is unlikely in the absence of land use or changes in vegetation distribution.

Key words. Soil organic carbon, global carbon cycle, climate change, greenhouse effect, model, parameterization, Terrestrial Ecosystem Model.

INTRODUCTION

Terrestrial ecosystems are thought to contain approximately 1500 Pg C (10¹⁵ g carbon) in soil organic matter (Schlesinger, 1977; Post *et al.*, 1982; Eswaran, Van Den Berg & Reich, 1993), which is about twice the carbon in the atmosphere (Watson *et al.*, 1990). Carbon is transferred from soils to the atmosphere predominantly in the form of CO₂ through the process of decomposition; this flux is approximately 50 Pg C annually (Watson *et al.*, 1990). A dominant feature of climate change predicted by general circulation models (GCMs) for a doubled CO₂ atmosphere is an increase in mean surface temperature of the globe (Mitchell *et al.*, 1990). Because decomposition is a temperature-sensitive process (Peterjohn *et al.*, 1993, 1994; Kicklighter *et al.*, 1994), elevated temperature has the

potential to increase the flux of CO₂ from soils to the atmosphere. However, if plant production increases in response to climate change (see Melillo *et al.*, 1993), then the removal of carbon from the atmosphere may be enhanced. Thus, climate change has the potential to either accelerate or slow the build-up of atmospheric CO₂ depending on how it influences both decomposition and plant production. Clearly, assessments of the influence of climate change on the atmospheric concentration of CO₂ require models that can integrate the effects of climate change on carbon storage in the terrestrial biosphere.

In this study we use a new version of the Terrestrial Ecosystem Model (TEM), which is a process-based model that has previously been used to assess the effects of climate change and elevated CO₂ on soil organic carbon (SOC; Melillo *et al.*, 1995; McGuire, Kicklighter &

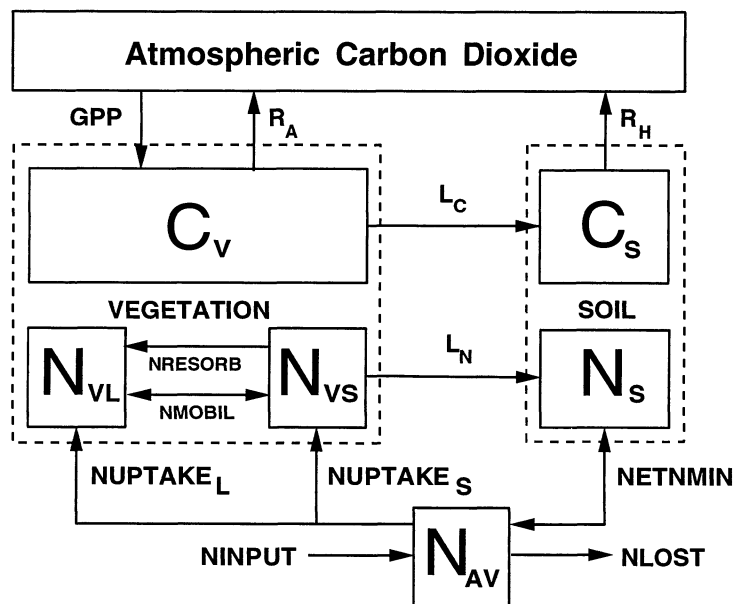


FIG. 1. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation (C_V); structural nitrogen in the vegetation (N_{VS}); labile nitrogen in the vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic nitrogen in soils and detritus (N_S); and available soil inorganic nitrogen (N_{AV}). Arrows show carbon and nitrogen fluxes; GPP , gross primary productivity; R_A , autotrophic respiration; R_H , heterotrophic respiration; L_C , litterfall carbon; L_N , litterfall nitrogen; $NUPTAKE_S$, nitrogen uptake into the structural nitrogen pool of the vegetation; $NUPTAKE_L$, nitrogen uptake into the labile nitrogen pool of the vegetation; $NRESORB$, nitrogen resorption from dying tissue into the labile nitrogen pool of the vegetation; $NMOBIL$, nitrogen mobilized between the structural and labile nitrogen pools of the vegetation; $NETNMIN$, net nitrogen mineralization of soil organic nitrogen; $NINPUT$, nitrogen inputs from outside the ecosystem; and $NLOST$, nitrogen losses from the ecosystem.

Melillo, 1995), to evaluate the sensitivity of SOC to a 1°C warming in both empirical and process-based analyses. In the empirical analyses, we evaluate the sensitivity of SOC to warming by extrapolating across the terrestrial biosphere empirical models of SOC response to warming; the empirical models are based on the steady state process-based SOC estimates of TEM for contemporary climate and atmospheric CO_2 and include the effects of temperature and soil moisture. In the process-based analyses we estimate SOC change by the difference between the pool sizes of SOC estimated by TEM for contemporary climate and the warming scenario. We also document the influence of elevated CO_2 on SOC estimates of TEM. Finally, we examine the potential implications of SOC response for the global carbon cycle.

MODEL DESCRIPTION AND METHODS

The TEM uses spatially referenced information on climate, soils, and vegetation to make monthly estimates of important carbon and nitrogen fluxes and pool sizes (Fig. 1). The first two versions of TEM were used to examine patterns of net primary production (NPP) in South America (Raich *et al.*, 1991) and North America (McGuire *et al.*, 1992). The third version of TEM was used to examine the response of net primary production (NPP) to elevated temperature and carbon dioxide for temperate forests (McGuire *et al.*, 1993) and to climate change predicted by general circulation models (GCMs) for the terrestrial biosphere (Melillo *et al.*,

1993). The carbon storage predictions of the third version were also evaluated for global terrestrial ecosystems (Melillo *et al.*, 1995) and for grasslands and conifer forests (McGuire *et al.*, 1995). In this study we use a new version of TEM (version 4.0), which we developed to improve patterns of carbon storage along gradients of temperature, moisture and soil texture.

In this paper we describe the modifications to the model that define version 4.0 of TEM, but the details of how the changes were implemented will appear elsewhere. Some of the modifications to TEM alter the effects of temperature, moisture and soil texture on model operation. The temperature modifications influence the equation for gross primary production (GPP). To allow local temperature adaptation/acclimation for carbon uptake, the optimum temperature of GPP is defined by the mean monthly temperature that corresponds to the month of maximum leaf area. Also, the minimum and maximum temperature constraints for GPP are set so that they reflect the growing-season limits of the vegetation type.

The moisture modifications affect nutrient diffusion in the soil, the carbon to nitrogen ratio of vegetation in grasslands and the decomposition of soil organic matter. The diffusion component of nitrogen uptake by plants and microbes has been modified to depend on volumetric soil moisture instead of percentage saturation, which is more consistent with the treatment of nutrient diffusion in Papendick & Campbell (1981). The half-saturation constants for plant and microbial uptake were also modified to depend on

nitrogen concentration in the soil solution instead of area-defined inorganic nitrogen. The vegetation carbon to nitrogen ratio in grasslands now depends on water balance so that lower ratios occur in drier environments, which is similar to the ratio calculations of Parton *et al.* (1987). The effects of moisture on decomposition were modified so that they depend on volumetric soil moisture instead of percentage saturation and the direct effects of soil texture in the moisture–decomposition relationship have been removed. However, soil texture indirectly affects the relationship by influencing volumetric soil moisture.

In previous versions of the model, soil texture was handled as a categorical variable with five classes (sand, sandloam, loam, clayloam and clay). In this version we treat soil texture as a continuous variable based on the proportion of silt plus clay (PSIPLUSC). Relationships have been incorporated into TEM so that rooting depth, porosity, field capacity and wilting point all depend on the PSIPLUSC. In this version of TEM, the parameters for carbon and nitrogen uptake capacity by vegetation are linear functions of PSIPLUSC so that they represent how potential leaf area and potential fine root surface area varies with soil texture. The parameters for decomposition and immobilization capacity by microbes are inversely related to PSIPLUSC so that they represent the physical protection of soil organic matter in fine-textured soils.

A number of miscellaneous modifications are also implemented in this version of TEM. The mean state of decay of the most recent 6 years of litter inputs, which is D in the immobilization equation, has been modified so that it indicates the mean state of decay of SOC for which the proportion of mass remaining from the original litter input is more than 20%. In long-term studies of mass loss from litter cohorts, the dynamics of decomposition appear to qualitatively change as detritus passes from a fast to a slow pool (Aber, Melillo & McLaugherty, 1990); we chose 20% as the transition between a fast and a slow pool based on the data of Aber *et al.* (1990). To implement better control of the carbon to nitrogen ratio of soil organic matter, which is defined by the parameter S_{CN} , the equation for net nitrogen mineralization has been modified to depend on S_{CN} . The calculation for monthly net irradiance, i.e. the shortwave irradiance at the top of the canopy, has been modified to depend on the relationship of Black, Bonython & Prescott (1954) instead of Black (1956). Finally, in this version of TEM we restrict the labile nitrogen pool of the vegetation to be less than 20% of the structural nitrogen pool of the vegetation. This prevents the labile pool from getting unrealistically large, a problem we observed for only a handful of sites in our global extrapolations of TEM.

The data sets used in this study to run TEM (vegetation (Melillo *et al.*, 1993), elevation (NCAR/Navy, 1984), soil texture as percentage of silt plus clay (FAO/CSRC/MBL, undated), mean monthly temperature (Legates & Willmott, 1990a), monthly precipitation (Legates & Willmott, 1990b), and mean monthly percentage cloudiness (Hahn/CSRC/MBL, undated)) are gridded at a spatial resolution of 0.5° (latitude \times longitude). Hydrological inputs for TEM are determined by a water balance model (Vorosmarty *et al.*, 1989) that uses these variables. The application of TEM

to a grid cell requires the use of the monthly climatic and hydrological data and the soil- and vegetation-specific parameters appropriate to the grid cell. The soil-specific parameters define rooting depth, porosity, field capacity and wilting point. Although many of the vegetation-specific parameters are defined from published information (Raich *et al.*, 1991; McGuire *et al.*, 1992), some are determined by calibrating the model to the fluxes and pool sizes of an intensively studied field site that is representative of the vegetation type. Four vegetation types are not parameterized for TEM 4.0 because we consider them to be mosaics of other vegetation types: boreal woodland, temperate savanna, temperate mixed forest and tropical savanna. Boreal woodland is defined to consist of moist tundra and boreal forest, temperate savanna of tall grassland and temperate deciduous forest, temperate mixed forest of temperate deciduous forest and temperate conifer forest and tropical savanna of tall grassland and tropical deciduous forest. The model makes estimates for mosaic grid cells by equally weighting estimates made with each of the appropriate non-mosaic calibrations.

Table 1 indicates the calibration site of each of the non-mosaic vegetation types. Note that although there are fourteen non-mosaic vegetation types, there are only ten parameterizations because some of the vegetation types use the same parameterization. The values of annual NPP, NUPTAKE, C_V , vegetation carbon to nitrogen ratio (V_{CN}), C_S , and soil carbon to nitrogen ratio (S_{CN}) used to calibrate the model for the soil texture of the calibration site are documented in Table 1. Except for C_S , the studies used to determine these values are documented in McGuire *et al.* (1992) for most of the calibration sites.

The pool C_S , which we equate with SOC in the context of TEM, includes dead organic carbon in detritus and soils. The processes affecting C_S in TEM are appropriate for upland aerobic soils; anaerobic soil processes are not represented in the model. For grasslands, we used the equation of Burke *et al.* (1989) for non-cultivated soils to determine the 20 cm C_S appropriate for the soil texture of the Pawnee Grassland calibration site. Although the Burke equation technically is designed to estimate non-detrital dead organic carbon in soils of U.S. grasslands, our application of it for sandloam at the Pawnee site indicates that it may overestimate total dead organic carbon in detritus and soils by almost 20% when compared with information in Table 1 of Clark (1977). Because detritus is a minor component of dead organic carbon in short grasslands and there is substantial spatial variability in soil carbon within a 0.5° grid cell (Burke *et al.*, 1990, 1991), the use of the Burke equation to estimate total dead organic carbon in U.S. grasslands is well within the range of uncertainty and provides a spatially explicit comparison for TEM estimates of C_S in U.S. grasslands.

To control for soil carbon quality across climatic gradients, we determined values of C_S for other calibration sites so that transitions in SOC are smooth at ecosystem boundaries. This was accomplished by calibrating the vegetation-specific parameters of the model to several values of C_S , extrapolating each calibration near the ecosystem boundary of interest, and choosing the C_S that resulted in

TABLE 1. Study sites, fluxes and pools used to calibrate some of the vegetation-specific parameters for TEM 4.0.

Vegetation type	Calibration site	Latitude	Longitude	NPP	NUPTAKE	C _v	V _{cn}	C _s	S _{cn}
Polar desert/alpine tundra	Toolik Lake (U.S.A.)	68° 38' N	149° 34' W	65.0	0.5	450	69.23	6000	23.08
Wet/moist tundra	Toolik Lake (U.S.A.)	68° 38' N	149° 34' W	120.0	0.8	750	50.00	12000	16.36
Boreal forest	Bonanza Creek (U.S.A.)	64° 45' N	148° 15' W	220.0	2.3	9000	375.00	11000	29.73
Temperate coniferous forest	Harvard Forest (U.S.A.)	42° 32' N	72° 10' W	486.8	3.8	11300	403.57	7500	23.86
Desert	Curlew Valley (U.S.A.)	41° 05' N	113° 05' W	110.0	2.7	540	27.69	2500	11.90
Arid shrubland	Curlew Valley (U.S.A.)	41° 05' N	113° 05' W	110.0	2.7	540	27.69	2500	11.90
Short grassland	Pawnee Grassland (U.S.A.)	40° 49' N	104° 46' W	200.0	3.5	315	35.80	3436	11.12
Tall grassland	Pawnee Grassland (U.S.A.)	40° 49' N	104° 46' W	200.0	3.5	315	35.80	3436	11.12
Temperate deciduous forest	Harvard Forest (U.S.A.)	42° 32' N	72° 10' W	650.0	8.0	15500	420.27	7500	20.63
Temperate broadleaf evergreen forest	Taita (New Zealand)	41° 11' S	174° 58' E	850.0	10.4	15000	357.14	9600	25.78
Mediterranean shrubland	Guanica (Puerto Rico)	17° 55' N	66° 55' W	550.0	14.0	4300	47.78	5000	9.79
Xeromorphic forest	Guanica (Puerto Rico)	17° 55' N	66° 55' W	550.0	14.0	4300	47.78	5000	9.79
Tropical deciduous forest	Ducke (Brazil)	2° 50' S	59° 57' W	1050.0	24.0	22500	75.00	7000	16.03
Tropical evergreen forest	Ducke (Brazil)	2° 50' S	59° 57' W	1050.0	24.0	22500	75.00	7000	16.03

Units for annual net primary production (NPP) and annual nitrogen uptake (NUPTAKE) are $\text{gC m}^{-2} \text{yr}^{-1}$ and $\text{gN m}^{-2} \text{yr}^{-1}$, respectively. Units for vegetation carbon (C_v) and soil carbon (C_s) are gC m^{-2} . The vegetation C to N ratio (V_{cn}) and soil C to N ratio (S_{cn}) are unitless.

the smoothest SOC transition with the extrapolation of the calibration for the neighbouring vegetation type. This technique is intended to standardize the climatic and edaphic reactivity of SOC across all calibration sites to the reactivity at the Pawnee site. Soil carbon deeper than 20 cm at the Pawnee site is predominantly Pleistocene in origin (David Schimel, pers. comm.), and is presumably unreactive in the context of near-term climate change. The standardization procedure allows us to ignore similarly unreactive SOC at all calibration sites, with the assumption that transitions in reactive SOC are smooth across ecosystem boundaries. Therefore, the SOC estimates of TEM represent only reactive SOC where reactive SOC is defined by 20 cm SOC at the Pawnee Grassland site.

The baseline run for each grid cell starts with the December values from the appropriate vegetation-specific calibration (see Table 1). To determine a solution for baseline conditions, the model is run with an open nitrogen cycle and nitrogen is annually imported or exported through the inorganic nitrogen pool depending on whether soil organic matter is nitrogen poor or rich in comparison with S_{CN} , the carbon to nitrogen ratio of the soil at the calibration site. This algorithm simulates the balance between long-term nitrogen inputs and outputs so that the grid cell has an equilibrium soil carbon to nitrogen ratio equal to S_{CN} ; it has the benefit of reaching equilibrium much faster than explicitly simulating nitrogen fixation, nitrogen deposition, denitrification and nitrogen leaching losses.

In this study the baseline scenario is defined as contemporary climate at an atmospheric concentration of 312.5 p.p.m.v. CO_2 . We use 312.5 p.p.m.v. CO_2 because it is the baseline concentration for the GCM-defined climate change that we have used in previous studies (see Melillo *et al.*, 1993). The grid cell is determined to have reached equilibrium when the annual fluxes of NPP, L_C , and R_H differ by less than $1 \text{ gC m}^{-2} \text{ yr}^{-1}$, those of NETNMIN, L_N and NUPTAKE differ by less than $0.02 \text{ gN m}^{-2} \text{ yr}^{-1}$, and those of NINPUT and NLOST differ by less than $0.02 \text{ gN m}^{-2} \text{ yr}^{-1}$. Because NINPUT and NLOST are determined annually, these fluxes are effectively 0 at equilibrium.

To run a grid cell for an altered climate or elevated CO_2 scenario, the initial values of the pools for the grid cell are set to the December values of the equilibrium baseline solution for the grid cell. The nitrogen cycle is closed for the run so that there is no nitrogen imported or exported from the grid cell. For the 1°C warming scenarios we added 1°C to each monthly temperature in the temperature data set used to run TEM. For the elevated- CO_2 scenario we use 625.0 p.p.m.v., which is twice the concentration of the baseline scenario. The conditions for determining when the grid cell has come to equilibrium are the same as for the baseline solution.

GLOBAL EXTRAPOLATION FOR CONTEMPORARY CLIMATE

For contemporary climate at an atmospheric concentration of 312.5 p.p.m.v. CO_2 , TEM estimates the reactive pool of global SOC to be 706.5 Pg (Table 2). Approximately 29%

of the SOC occurs in the tropical ecosystems (207.6 Pg), 31% in the temperate ecosystems (219.1 Pg) and 40% in boreal ecosystems (279.8 Pg). Boreal forest, which covers 9.5% of the terrestrial land area, accounts for the most SOC (18.3% of global SOC). Tropical evergreen forest also accounts for a substantial proportion of global SOC (15.1%). Desert, which covers 9.0% of the terrestrial surface, accounts for the least (0.7%). Mean SOC densities for ecosystems range from 436 g m^{-2} in desert to 11211 g m^{-2} in boreal woodland (Table 2). Estimates for individual grid cells range from 1 g m^{-2} in desert to 20970 g m^{-2} in boreal woodland (Table 2).

To examine the influence of temperature and moisture on the reactive SOC estimates of TEM, we analyse the estimates along transects that are continuous transitions of temperature or precipitation and that cut across a variety of ecosystems. Along a temperature gradient in eastern Asia at 110°E , estimates of SOC gradually increase from tropical evergreen forest in the south to moist tundra in the north and decline for polar desert (Fig. 2). The estimates of SOC between latitudes 38°N and 48°N are lower as the transect crosses the grasslands of the Mongolian plateau where precipitation ranges between 149 and 482 mm yr^{-1} . Thus, in moist environments SOC gradually increases because decomposition declines more rapidly with decreasing temperature than does NPP. In polar desert SOC drops with decreasing temperature because NPP declines more rapidly than does decomposition.

Along a precipitation gradient in temperate North America at 41.5°N , estimates of SOC decline west to east with decreasing precipitation as the vegetation changes from maritime conifer forests to arid shrublands (Fig. 3). Estimates then rise with increasing precipitation west to east through grasslands, temperate savanna, and eastern forests. As the transect crosses the Great Plains, the estimates of TEM are similar to the estimates of the regression model developed by Burke *et al.* (1989) for non-cultivated soils; the Burke model considers mean annual temperature, annual precipitation and soil texture. Across the Great Plains of the United States, the estimates of TEM are similar to those estimated by the Burke model ($R = 0.846$, $n = 525$, $P < 0.0001$). Thus, TEM estimates that within a similar thermal regime SOC generally declines with decreasing precipitation.

THE SOC RESPONSES OF THE EMPIRICAL MODELS

We used multiple linear regression to fit the dependent variable $\ln(\text{SOC})$ to the independent variables mean annual temperature (T) and mean volumetric soil moisture as determined by the water balance model of TEM (V). For all SOC estimates of TEM applied across the terrestrial biosphere ($n = 56389$) at 312.5 p.p.m.v. and contemporary climate, T explains 34.8% of the variance in $\ln(\text{SOC})$ and the inclusion of V explains an additional 19.6%. Because V helps to explain more of the variability in SOC, the use of a moisture term in an empirical model of SOC response to warming should improve response estimates. To derive a response equation for a 1°C warming that has the form

TABLE 2. Estimates by TEM 4.0 of reactive soil organic carbon (SOC) for potential vegetation in the terrestrial biosphere for contemporary climate at an atmospheric concentration of 312.5 p.p.m.v. CO₂.

Vegetation type	Area 10 ⁶ km ⁻²	Cells	Total SOC 10 ¹⁵ gC	Mean SOC	Max SOC gC m ⁻²	Min SOC
Polar desert/alpine tundra	5.1	3338	26.1	5108	14123	22
Wet/moist tundra	4.9	3896	54.3	11161	15800	99
Boreal woodland	6.3	4414	70.4	11211	20970	2573
Boreal forest	12.2	7406	129.0	10601	17373	958
Temperate coniferous forest	2.4	1081	18.7	7803	12938	1772
Desert	11.5	4145	5.0	436	4048	1
Arid shrubland	14.5	5708	26.5	1828	6413	82
Short grassland	4.7	2050	19.1	4095	7919	851
Tall grassland	3.6	1557	16.9	4695	8165	772
Temperate savanna	6.8	2886	33.3	4935	9958	552
Temperate mixed forest	5.1	2250	39.1	7675	13413	3313
Temperate deciduous forest	3.5	1614	30.7	8642	15632	883
Temperate broadleaf evergreen forest	3.2	1205	23.1	7257	14550	2264
Mediterranean shrubland	1.4	554	6.7	4749	13160	353
Tropical savanna	13.7	4624	47.3	3443	8265	548
Xeromorphic forest	6.8	2357	32.2	4760	18665	4
Tropical deciduous forest	4.6	1577	21.3	4633	9579	409
Tropical evergreen forest	17.4	5727	106.8	6148	9687	1893
Total	127.7	56389	706.5	5532	20970	1

$A_e^{(bT+cV)}$, we took the partial derivative of SOC(T,V) with respect to temperature where SOC(T,V) was determined from the regression of $\ln(\text{SOC})$ with T and V. This globally derived empirical model estimates the sensitivity of global SOC to be a loss of 22.6 Pg for a 1 °C warming (Table 3). Of the loss, the global empirical model estimates a carbon loss of 17.6 Pg (77.9%) for the extra-tropical ecosystems and 5.0 Pg (22.1%) for tropical ecosystems; tropical ecosystems are defined as tropical savanna, xeromorphic forest, tropical deciduous forest and tropical evergreen forest.

To explore whether loss estimates of SOC are affected by the spatial scale at which the response equations are derived, we derived equations for each of the eighteen ecosystems considered in this study. The ecosystem empirical models have some features in common, but differ in other aspects (Table 3). All the coefficients with T are negative and range from -0.1402 in mediterranean shrublands to -0.0199 in boreal woodland. The coefficients of V are all positive except for mediterranean shrubland and temperate broadleaf evergreen forest; among all vegetation types the relationship between $\ln(\text{SOC})$ and V for these ecosystems are the only ones that are not significant. Thus, the models generally estimate higher SOC losses for lower temperature and for higher soil moisture. Among the ecosystem empirical models, the variance in $\ln(\text{SOC})$ explained by T ranges from 14.3% in temperate broadleaf evergreen forest to 63.1% in temperate deciduous savanna, and the additional variance explained by V ranges from 0.1% in temperate broadleaf evergreen forest to 24.7% in xeromorphic forest. In general, the ecosystem empirical models estimate that SOC losses within ecosystems are more sensitive to increasing temperature than to decreasing soil moisture.

The sensitivity of terrestrial SOC estimated by summing the losses predicted by each of the ecosystem empirical models is greater (27.9 Pg per °C) than that estimated by the global empirical model. The 15.7 Pg loss (56.3%) estimated for extra-tropical ecosystems is similar to that of the global empirical model (17.6 Pg). However, the 12.2 Pg loss (43.7%) for tropical ecosystems is substantially greater than that estimated by the global empirical model (5.0 Pg), and suggests that SOC in the tropics may be more sensitive to warming. Thus, globally derived empirical models of SOC response may conceal regional sensitivity of soil carbon stocks to warming.

THE PROCESS-BASED SOC RESPONSES OF TEM

For a 1 °C warming at 312.5 p.p.m.v. CO₂, TEM estimates a process-based SOC loss of 26.3 Pg (Table 4), which is similar to the 27.9 Pg loss estimated by the sum of the ecosystem empirical models. The 26.3 Pg SOC loss is divided between 13.6 Pg (51.7%) for extra-tropical ecosystems and 12.7 Pg (48.3%) for tropical ecosystems, which is more similar to the pattern of the ecosystem empirical models than to the pattern of the global empirical model. Similar to the ecosystem empirical responses, the process-based responses of TEM suggest that tropical SOC carbon may be more sensitive to warming than do the global empirical responses. However, the process-based responses suggest that extra-tropical SOC may be slightly less sensitive than do the ecosystem empirical responses. The process-based responses, similar to the ecosystem empirical responses, suggest that globally derived empirical models of SOC response may conceal regional sensitivity to warming.

For doubled CO₂ and no temperature change, TEM

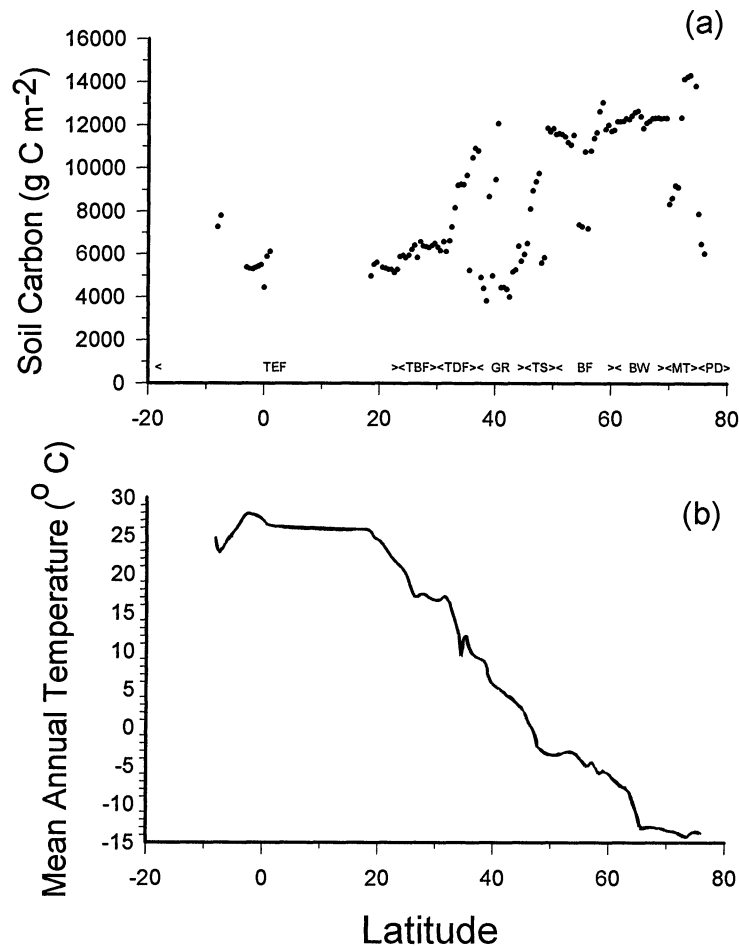


FIG. 2. For 124 grid cells (0.5° spatial resolution) along a south–north transect at 110°E , (a) the estimates of soil organic carbon by version 4.0 of the Terrestrial Ecosystem Model and (b) the mean annual temperature from the temperature data used to drive the model. Abbreviations: TEF, tropical evergreen forest; TBF, temperate broadleaf evergreen forest; TDF, temperate deciduous forest; GR, tall and short grasslands; TS, temperate savanna; BF, boreal forest; BW, boreal woodland; MT, moist tundra; and PD, polar desert.

estimates terrestrial SOC to increase by 40.9 Pg (Table 4). With a 1°C warming accompanying elevated CO_2 , TEM estimates a substantial increase in SOC of 28.4 Pg (Table 4). Thus, the process-based responses of TEM suggest that the effects of elevated CO_2 in enhancing NPP have the potential to more than compensate for potential SOC losses from warming.

DISCUSSION

The estimate of global reactive SOC in this study (706.5 Pg), which in the context of TEM includes both detrital and non-detrital dead organic carbon, is less than 50% of the approximately 1500 Pg estimated by several inventories of SOC to 1 m depth (Schlesinger, 1977; Post *et al.*, 1982; Eswaran *et al.*, 1993), and suggests that a substantial portion of the global inventory is unreactive with respect to near-term climate change. The TEM estimate of global reactive SOC is 14% higher than the 619.5 Pg of total dead organic carbon in detritus and soils to 30 cm

depth estimated by Potter *et al.* (1993) for the terrestrial biosphere. The reactive carbon estimated by Potter *et al.* (1993) for temperate latitudes between 30° and 60° (both north and south of the equator) is 37% of the total and is similar to the 31% estimated by TEM for temperate ecosystems. However, the estimate of 44% for tropical latitudes between 30°N and 30°S is substantially higher than the 29% estimated by TEM for tropical ecosystems; the 19% for boreal latitudes greater than 60°N is substantially less than the 40% estimated by TEM for boreal ecosystems. The differences in both magnitude and distribution of reactive SOC are presumably caused by differences in how the models are parameterized. Therefore, it is expected that empirical models derived from simulated SOC estimates based on depth criteria will differ from empirical models derived from the SOC estimates of TEM, which is calibrated with a procedure designed to standardize reactive SOC across calibration sites.

Recently, Schimel *et al.* (1994) analysed the sensitivity of SOC to a 1°C warming by extrapolating across the

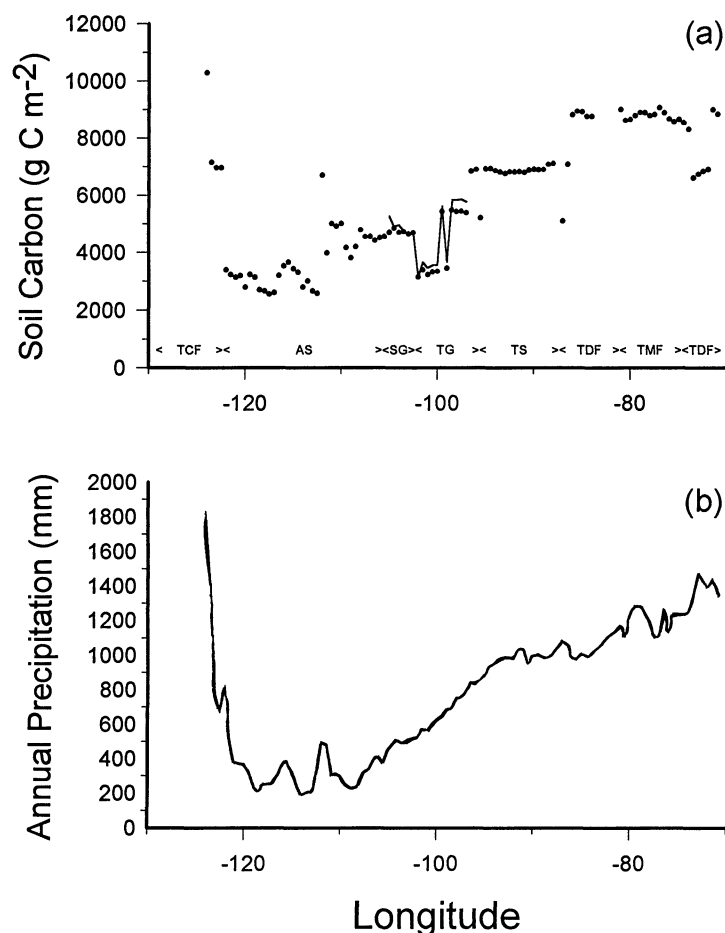


FIG. 3. For 101 grid cells (0.5° spatial resolution) along a west–east transect at 41.5°N , (a) the estimates of soil organic carbon by version 4.0 of the Terrestrial Ecosystem Model and (b) the annual precipitation from the precipitation data used to drive the model. The solid line in (a) indicates the soil organic carbon estimates of the regression model developed by Burke *et al.* (1989) for non-cultivated soils of the Great Plains. Abbreviations: TCF, temperate coniferous forest; AS, arid shrubland; SG, short grassland; TG, tall grassland; TS, temperate savanna; TDF, temperate deciduous forest; and TMF, temperate mixed forest.

terrestrial biosphere at 0.5° spatial resolution two empirical models of SOC response that both have the form Ae^{bT} ; the models depend only on mean annual temperature. They reported the sensitivity of SOC to be losses of 11.1 Pg per $^\circ\text{C}$ (based on simulations of 20-cm SOC by the CENTURY model) and 14.1 Pg per $^\circ\text{C}$ (based on 20-cm SOC observations assembled for Buol *et al.*, 1990). The elimination of histosols, deserts and arid shrublands from the extrapolation of the empirical model based on CENTURY simulations yields an estimated SOC loss of 11.7 Pg, which is similar to the 11.1 Pg loss; Schimel *et al.* (1994) actually eliminated histosols and aridisols.

When we extrapolate the empirical model based on the CENTURY simulations (i.e. the CENTURY empirical model) for the grid cells considered in this study, the 15.7 Pg loss of SOC to a 1°C warming is 30.5% lower than the 22.6 Pg loss estimated by the global empirical model of this study. The estimate may be lower, in part, because the CENTURY empirical model is calibrated for only non-detrital dead organic carbon. Also, the SOC simulations to

30 cm depth by Potter *et al.* (1993) suggest that 20-cm SOC simulations should consider less reactive carbon than TEM-estimated SOC. Of the global loss estimated by the CENTURY empirical model, 77.7% is in extra-tropical ecosystems and 22.3% in tropical ecosystems, which is similar to the partitioning estimated by the global empirical model of this study (77.9% and 22.1%). The coefficient with mean annual temperature in the CENTURY empirical model ($b = -0.0340$) is similar to that of the global empirical model in this study ($b = -0.0362$), and entering the average value for the mean annual volumetric soil moisture of grid cells in short grassland (20.3%) into the global empirical model produces a model ($-188.7e^{-0.0362T}$) which is very similar to the CENTURY empirical model ($-183.0e^{-0.0340T}$). Therefore, the difference in global estimates of SOC loss between the two models may, in part, be related to the inclusion of the soil moisture term into the global empirical model of this study.

Although the addition of a moisture term to the globally derived empirical model is expected to improve estimates

TABLE 3. Estimates of soil organic carbon (SOC) responses for the terrestrial biosphere to a 1°C warming based on the partial derivative of SOC with respect to mean annual temperature.

Vegetation type	Cells (n)	Response of global empirical model ¹			Response of ecosystem empirical models ³		
		10 ¹⁵ gC	A	b	c	R ²	10 ¹⁵ gC
Polar desert/alpine tundra	3338	-1.5	-49.10	-0.0335	0.0439	0.668	-0.7
Wet/moist tundra	3896	-1.9	-113.34	-0.0206	0.0209	0.576	-1.1
Boreal woodland	4414	-2.5	-166.16	-0.0199	0.0063	0.696	-1.4
Boreal forest	7406	-4.2	-184.36	-0.0267	0.0143	0.768	-3.4
Temperate coniferous forest	1081	-0.5	-270.84	-0.0341	0.0122	0.737	-0.6
Desert	4145	-0.6	-139.35	-0.1058	0.0627	0.420	-0.4
Arid shrubland	5708	-1.2	-259.18	-0.0719	0.0166	0.779	-1.7
Short grassland	2050	-0.7	-96.35	-0.0320	0.0256	0.657	-0.6
Tall grassland	1557	-0.7	-60.99	-0.0268	0.0395	0.680	-0.4
Temperate savanna	2886	-1.1	-474.74	-0.0654	0.0102	0.797	-2.1
Temperate mixed forest	2250	-1.1	-169.56	-0.0274	0.0192	0.806	-1.1
Temperate deciduous forest	1614	-0.8	-241.44	-0.0295	0.0119	0.695	-0.9
Temperate broadleaf evergreen forest	1205	-0.7	-262.07	-0.0242	-0.0012	0.380	-0.5
Mediterranean shrubland	554	-0.1	-8382.38	-0.1402	-0.0211	0.596	-0.8
Tropical savanna	4624	-1.2	-1730.16	-0.0917	0.0222	0.796	-4.2
Xeromorphic forest	2357	-0.6	-259.77	-0.0590	0.0583	0.665	-1.7
Tropical deciduous forest	1577	-0.5	-3377.34	-0.0930	0.0082	0.675	-2.0
Tropical evergreen forest	5727	-2.7	-438.51	-0.0409	0.0159	0.634	-4.3
Total	56389	-22.6	—	—	—	—	-27.9

¹The response of the global empirical model for which the partial derivative of SOC with respect to temperature is $-34.51e^{-0.0362T}e^{0.0837V}$ where T is mean annual temperature and V is mean annual volumetric soil moisture as calculated by the water balance model of TEM 4.0. ²The correlation coefficient from the linear relationship of $\ln(\text{SOC})$ with T and V. ³The response of the ecosystem empirical models for which the partial derivative of SOC with respect to temperature is $Ae^{(bT+cV)}$.

of SOC loss, it does not eliminate bias. The concealment of regional sensitivity of SOC loss warns against the use of globally derived empirical models to assess regional SOC responses. Also, the 5.3 Pg difference between the global response of the ecosystem empirical models and that of the global empirical model suggests that the latter may underestimate SOC response at the global scale by nearly 20%. Potential problems of bias should be assessed before extrapolating globally derived empirical models across either global or regional scales.

Both the global and regional SOC responses of the ecosystem empirical models and the process-based TEM are, in general, similar. Although this is reassuring, it must be recognized that the responses may be sensitive to assumptions about the reactivity of dead organic matter. One of the difficulties in modelling the response of soil carbon to climate change is that the flux from dead organic matter is dominated by young, more easily decomposed cohorts derived from vegetation litterfall (Melillo *et al.*, 1989; Aber *et al.*, 1990; Schimel *et al.*, 1994), whereas a substantial proportion of soil carbon is in older cohorts that are composed of refractory organic compounds and are resistant to decomposition (Trumbore, Bonani & Wolfi, 1990; Harrison, Broecker & Bonani, 1993). The variability in the decomposability of soil organic matter poses a time-scale problem for models that produce equilibrium solutions to assess the effects of climate change on carbon storage. If cohorts with turnover times much greater than the expected

time-scale of climate change are included in the analysis, then there is the potential to overestimate the response of carbon storage. For example, for doubled-CO₂ climates predicted by four GCMs, version 3 of the TEM, which was calibrated for soil carbon to 1 m depth, predicts decreases in SOC to vary between 180 and 211 Pg C at 312.5 p.p.m.v. CO₂ (Melillo *et al.*, 1995). However, when the model was parameterized for 20 cm soil carbon, the decreases vary between 84 and 128 Pg C (Melillo *et al.*, 1995); the response of plant production was insensitive to calibration depth. The soil carbon response of the 20 cm calibration may be more appropriate to shorter-term climatic change than is the 1 m calibration. Thus, the sensitivity of soil carbon to calibration depth indicates the importance of identifying the carbon that is likely to be actively decomposing over the time-scale of climatic change (McGuire *et al.*, 1995).

Because much soil carbon is derived from aboveground inputs of plant litter, depth is a convenient means of separating young cohorts of soil carbon from old cohorts. However, depth may not be the most reliable metric because soil carbon can be derived from sensing roots at many depths. Some analyses of the response of soil carbon to climate change have used a depth of 20 cm for parameterization (Schimel *et al.*, 1990; Ojima *et al.*, 1993; Schimel *et al.*, 1994). These analyses have evolved from the study of soil carbon storage in grasslands with the CENTURY model (Parton *et al.*, 1987). A depth of 20 cm may be more

TABLE 4. Estimates by TEM 4.0 of soil organic carbon (SOC) responses for the terrestrial biosphere to a 1°C warming and/or doubling the atmospheric concentration of CO₂ from 312.5 p.p.m.v. to 625.0 p.p.m.v.

Vegetation type	Area 10 ⁶ km ²	Cells	Total SOC 10 ¹⁵ gC	+ 0°C		
				+ 1°C 312.5 p.p.m.v.	625.0 p.p.m.v. response (10 ¹⁵ gC)	+ 1°C 625.0 p.p.m.v.
Polar desert/alpine tundra	5.1	3338	26.1	-0.9	+2.0	+1.3
Wet/moist tundra	4.9	3896	54.3	-0.2	+1.5	+1.6
Boreal woodland	6.3	4414	70.4	-0.8	+2.3	+2.4
Boreal forest	12.2	7406	129.0	-1.5	+3.9	+3.7
Temperate coniferous forest	2.4	1081	18.7	-0.6	+1.4	+1.1
Desert	11.5	4145	5.0	-0.4	+1.5	+1.3
Arid shrubland	14.5	5708	26.5	-1.6	+5.7	+4.9
Short grassland	4.7	2050	19.1	-0.4	+0.8	+0.6
Tall grassland	3.6	1557	16.9	-0.3	+0.7	+0.5
Temperate savanna	6.8	2886	33.3	-1.1	+2.4	+1.8
Temperate mixed forest	5.1	2250	39.1	-3.5	+2.7	+2.0
Temperate deciduous forest	3.5	1614	30.7	-1.0	+1.5	+1.1
Temperate broadleaf evergreen forest	3.2	1205	23.1	-1.0	+1.5	+1.1
Mediterranean shrubland	1.4	554	6.7	-0.3	+1.1	+0.9
Tropical savanna	13.7	4624	47.3	-2.3	+3.0	+1.3
Xeromorphic forest	6.8	2357	32.2	-2.8	+5.8	+4.5
Tropical deciduous forest	4.6	1577	21.3	-1.0	+0.8	+0.0
Tropical evergreen forest	17.4	5727	106.8	-6.6	+2.3	-1.7
Total	127.7	56389	706.5	-26.3	+40.9	+28.4

appropriate for grasslands than for forests, where rooting depth is generally deeper.

One argument for using 20 cm as a calibration depth in forests is that the mean ¹⁴C mean residence time for carbon to 20 cm in some measured German soils is between 200 and 600 years (Parton *et al.*, 1995). Because the ¹⁴C mean residence time has been measured with depth for only a few soil samples, more data are needed before this justification can be generalized for temperate forests. Even if the 20-cm calibration assumption could be generalized for temperate forests, it is unlikely that it could be extended to boreal and tropical systems because age does not control well for the reactivity of SOC along latitudinal gradients. Because 100-year-old carbon in a boreal forest should be less decomposed than 100-year-old carbon in a moist tropical forest, it should be a higher quality substrate for microbial decomposers.

Our technique of starting with 20 cm SOC in short grasslands for calibration and adjusting the SOC at other calibration sites so that transitions of SOC estimates are smooth across ecosystem boundaries is an attempt to control for the reactivity of SOC across climatic gradients. The higher responses of the TEM empirical and process-based analyses compared to the CENTURY empirical analysis may, in part, be related to differences in parameterizing the models. The control of soil carbon reactivity should be considered in the parameterization of either empirical or process-based models of SOC response to global change.

Although there is some controversy concerning the parameterization of empirical and process-based models, analyses based on different assumptions and different

models help to quantify some of the uncertainty in the response of SOC to climate change. The responses of empirical models reported in this study and of Schimel *et al.* (1994) suggest that the maximum loss of SOC to the atmosphere per °C warming is between 10 Pg and 30 Pg. These analyses do not consider the effects of elevated CO₂ on SOC, and therefore have limited predictive or prognostic capabilities. However, they are useful in a diagnostic sense because they indicate that equilibrium losses of SOC per °C warming are likely to be less than 2% of the global soil carbon inventory. A small enhancement of NPP in response to elevated CO₂ appears capable of compensating for this loss, either for a 1°C warming as analysed in this study or for warming predicted by GCMs to accompany elevated CO₂ (Melillo *et al.*, 1995; McGuire *et al.*, 1995). These process-based analyses suggest that there is little potential that warming will enhance carbon loss to the atmosphere to further enhance warming (see Houghton & Woodwell, 1989), at least for upland soils. The response of wetland soils to warming is not well understood, but the transition of soils from anaerobic to aerobic conditions may release substantial amounts of carbon to the atmosphere (Oechel *et al.*, 1993). Also, substantial carbon losses from terrestrial ecosystems could occur in the near-term from land use (Houghton *et al.*, 1983, 1987; Melillo *et al.*, 1988) and from changes in vegetation distribution associated with climate change (Smith & Shugart, 1993). Further progress in modelling the carbon exchange between the terrestrial biosphere and the atmosphere in an elevated-CO₂ world requires considering at large spatial scales the transient dynamics of carbon storage in response to climate, vegetation, and land-use changes.

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