

An equilibrium model of the terrestrial carbon budget

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ABSTRACT

The global terrestrial carbon budget is examined using a process-based model, DEMETER-1. In this version of the model, the carbon budgets of vegetation, litter and soil organic matter are simulated using simplified parameterizations of ecosystem processes and their climatic sensitivity. For the modern climate, the model simulates the carbon storage potential of the terrestrial biosphere: 800 Gt-C in vegetation, 150 Gt-C in litter and 1370 Gt-C in soil organic matter. The global and continental-scale simulations of net primary productivity and carbon storage are in good agreement with available observations. In particular, simulated biome-average soil carbon densities are in very strong agreement ($r = 0.9373$) with published data. To obtain accurate simulations on the local and regional scales, more detailed treatments of ecosystem processes may be required, provided that they can be validated across the range of spatial and temporal scales.

1. Introduction

Recently, a great deal of attention had been focused on the anthropogenic perturbations to the global carbon cycle and their possible consequences on the climate system. On the time scales in question, several decades to a few centuries, carbon is cycled between the atmosphere, oceans and the terrestrial biosphere. In order to properly diagnose the current state of the anthropogenic carbon budget and to predict its possible future course, the terrestrial component of the global carbon cycle must be examined further. In this study, the terrestrial carbon budget is simulated using a simple process-based model, DEMETER (Foley, 1994).

DEMETER is one of several published terrestrial carbon budget models (Raich et al., 1991; McGuire et al., 1992; Melillo et al., 1993; Potter et al., 1993). The current version of the model, DEMETER-1, differs from many other terrestrial biosphere models because: (1) it is primarily concerned with the dynamics of terrestrial carbon pools and does not consider the associated dynamics of mineral nutrients (e.g.,

nitrogen, phosphorus), and (2) it predicts, rather than prescribes, potential vegetation cover following the methodology of Prentice et al. (1992). Because it does not simulate carbon and nutrient interactions, DEMETER may be used to examine and isolate the climatic controls on terrestrial carbon stores. The climatic parameterizations used by the model are intentionally simplified to aid the interpretation of the results. This model design has an added advantage: DEMETER has far fewer parameters than some other terrestrial biosphere models.

2. Model description

DEMETER-1 operates at the global scale at a spatial resolution of 1° by 1° and simulates the flow of carbon through vegetation, litter and soil organic matter (Fig. 1). Carbon uptake by vegetation is simulated by a model of net primary productivity (NPP) (Foley, 1994). Vegetation carbon is lost through litterfall, defined here as the total loss of plant material. All litter of a given type is placed in a single compartment, where decom-

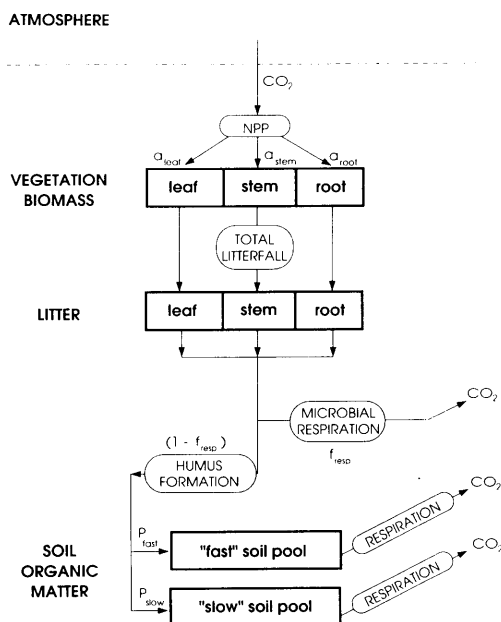


Fig. 1. The flow of carbon through the terrestrial biosphere as simulated by DEMETER-1.

position releases humus which enters the soil. Humus flowing into the soil is divided into two pools (fast and slow), with nearly all of the carbon entering the fast pool. In this study, DEMETER simulates only the equilibrium terrestrial carbon budget. A total accounting of the sources and sinks of terrestrial carbon yields no net balance: NPP is exactly matched by the sum of litter and soil organic matter decomposition.

2.1. Climate

The model simulates the surface energy and water balance from air temperature, precipitation and solar radiation (Leemans and Cramer, 1990). On the daily timestep, i , surface net radiation, $R_{\text{net},i}$, is calculated,

$$R_{\text{net},i} = \text{SW}_{\text{net},i} - \text{LW}_{\text{net},i} \quad (1)$$

where SW_{net} and LW_{net} are the terms for net downward shortwave and net upward longwave radiation. Net shortwave and longwave radiation are calculated from insolation, temperature and cloudiness data (Leemans and Cramer, 1990;

Linacre, 1986). Actual evapotranspiration, AET, is simulated as,

$$\text{AET}_i = \min \left(\frac{s}{s + \gamma} \frac{R_{\text{net},i}}{L}, \text{AET}_{\text{max}} \frac{M_i}{M_{\text{max}}} \right), \quad (2)$$

where AET_{max} is the maximum rate of evapotranspiration, M_i is the daily soil moisture content, M_{max} is the soil moisture content at saturation, L is the latent heat of vaporization, s is the rate of change of saturated water vapor pressure with respect to temperature, and γ is the psychrometer constant. Soil moisture obeys the following,

$$M_i = \min((M_{i-1} + (P_i - \text{AET}_i)), M_{\text{max}}), \quad (3)$$

where P_i is the daily precipitation. If the simulated soil moisture exceeds M_{max} , then the model records the difference as runoff.

2.2. Potential vegetation

Potential vegetation cover is simulated following the BIOME model of Prentice et al. (1992). Biomes are defined as combinations of plant functional types, whose geographic distribution is simulated as a function of the climate. The climatic variables used by the model include growing degree days above 0°C and 5°C bases, the temperature of the coldest month, the temperature of the warmest month, and the annual moisture index, α_{annual} ,

$$\alpha_{\text{annual}} = \frac{1}{365} \sum_{i=1}^{365} \frac{\text{AET}_i}{\frac{s}{s + \gamma} \frac{R_{\text{net},i}}{L}} \quad (4)$$

2.3. Net primary productivity

Foley (1994) describes the NPP model in more detail; here the basic features of the model are presented. NPP is defined as,

$$\text{NPP} = \text{GPP} - R, \quad (5)$$

where GPP, gross primary productivity, is the amount of carbon fixed via photosynthesis (minus photorespiration), and R , autotrophic respiration, is the amount of carbon lost to maintain the existing biomass and to grow new tissues. GPP is calculated as,

$$\text{GPP} = \int_0^{\text{LAI}} P_0 \frac{\phi}{\phi + \frac{P_0}{I_{\text{PAR}} \exp(-kL)}} dL \quad (6)$$

where LAI is the leaf area index of the canopy, P_0 is the light saturated rate of photosynthesis on an incremental leaf layer, ϕ is the quantum efficiency of photosynthesis at low light intensity, I_{PAR} is the photosynthetically active radiation (PAR) intensity at the top of the canopy, k is the light extinction coefficient and L is the incremental leaf area (integrated from 0 to LAI). To account for the effects of climate and vegetation cover on photosynthesis, P_0 and ϕ are expressed as functions of air temperature, the moisture index and the metabolic pathway of the vegetation.

Respiration accounts for about half of the carbon fixed through photosynthesis (Ryan, 1991). The model divides R into functional components of maintenance and growth respiration (Amthor, 1986),

$$R = R_{\text{maint}} + R_{\text{growth}} \quad (7)$$

Respiration costs are calculated as a function of the vegetation cover and climate.

2.4. Vegetation biomass

At equilibrium, vegetation carbon, C_v , obeys,

$$\frac{\partial C_v}{\partial t} = \text{NPP} - \text{LF} - H = 0, \quad (8)$$

where LF is the biomass lost by total litterfall and H is the biomass lost by herbivory. Here, total litterfall is defined as the loss of vegetation biomass due to the mortality of vegetation (including leaf, stem and root tissues). In this study, herbivory is ignored,

$$\frac{\partial C_v}{\partial t} = \text{NPP} - \text{LF} = 0. \quad (9)$$

Values of C_v are obtained from the Olson et al. (1983) vegetation and carbon database (Table 1). While there are substantial regional variations in the amount of standing vegetation biomass, the model assumes that, on the mean, the Olson et al. estimates are representative.

Vegetation carbon is divided into three pools: leaf biomass, stem biomass and root biomass,

$$\sum_{j=1}^3 \frac{\partial C_{v,j}}{\partial t} = \sum_{j=1}^3 a_j \text{NPP} - \sum_{j=1}^3 \text{LF}_j = 0, \quad (10)$$

where the partitioning of NPP between leaf, stem and root tissues is represented by the a_j parameters, where j is an index of the biomass compartments (1: leaf, 2: stem, 3: root). Values of a_j (Table 1) were estimated from a review of the literature.

Table 1. Parameters of the DEMETER-1 carbon budget model

	Biome name	a_{leaf}	a_{stem}	a_{root}	f_{resp}	P_{fast}	P_{slow}
1	tropical rainforest	0.40	0.20	0.40	0.65	0.980	0.020
2	tropical seasonal forest	0.40	0.20	0.40	0.65	0.980	0.020
3	tropical dry forest & savanna	0.50	0.10	0.40	0.70	0.985	0.015
4	warm mixed forest	0.40	0.20	0.40	0.70	0.985	0.015
5	temperate deciduous forest	0.40	0.20	0.40	0.70	0.985	0.015
6	cool mixed forest	0.40	0.20	0.40	0.70	0.985	0.015
7	cool conifer forest	0.40	0.20	0.40	0.70	0.985	0.015
8	boreal forest	0.40	0.20	0.40	0.70	0.985	0.015
9	cold mixed forest	0.40	0.20	0.40	0.70	0.985	0.015
10	cold deciduous forest	0.45	0.15	0.40	0.70	0.985	0.015
11	xerophytic woods & scrub	0.50	0.10	0.40	0.70	0.985	0.015
12	warm grass & shrub	0.80	0.00	0.20	0.70	0.985	0.015
13	cool grass & shrub	0.80	0.00	0.20	0.70	0.985	0.015
14	tundra	0.65	0.05	0.30	0.70	0.985	0.015
15	hot desert	0.50	0.20	0.30	0.75	0.985	0.015
16	semidesert	0.50	0.20	0.30	0.75	0.985	0.015
17	ice & polar desert	0.00	0.00	0.00	0.00	0.000	0.000

a_{leaf} , a_{stem} and a_{root} represent the allocation of NPP into the biomass compartments, f_{resp} is the fraction of litter carbon that is released as CO_2 during decomposition, P_{fast} and P_{slow} are the fractions of humus that are sent to the fast and slow pools, respectively.

By fixing C_v and a_j for each biome, the following expression may be derived,

$$LF_j = a_j \text{ NPP}. \quad (11)$$

Eq. (11) is an expression of true equilibrium: the carbon coming into a vegetation biomass compartment (a_j NPP) is exactly equal to carbon leaving that compartment (LF_j).

2.5. Litter

Like vegetation carbon, litter is broken into three compartments: leaf, stem and root litter. DEMETER assumes that litter decomposition obeys a first-order rate decay equation,

$$\sum_{j=1}^3 \frac{\partial C_{l,j}}{\partial t} = \sum_{j=1}^3 LF_j - \sum_{j=1}^3 k_{l,j} C_{l,j} = 0, \quad (12)$$

where $C_{l,j}$ is the carbon stored in litter type j and $k_{l,j}$ is the decomposition coefficient for the litter pool. Under equilibrium conditions the time derivative term in eq. (12) drops out, leaving,

$$C_{l,j} = \frac{LF_j}{k_{l,j}}. \quad (13)$$

The rate at which litter decays is controlled by the climate and the quality of the vegetation material (Meentemeyer, 1978, 1984; Esser et al., 1982; Vogt et al., 1986; Upadhyay et al., 1989; Dyer et al., 1990). DEMETER adopts a very simple relationship between $k_{l,j}$, litter quality and climate (Meentemeyer, 1978 and 1984)

$$k_{l,j} = \varepsilon_j 10^{(-1.4553 + 0.0014175 \cdot \text{AET})}, \quad (14)$$

where AET is the annual actual evapotranspiration (mm yr^{-1}) and ε_j describes the relative ability of the litter types to decay ($\varepsilon_1 = 1.0$, $\varepsilon_2 = 0.5$, $\varepsilon_3 = 2.0$).

2.6. Soil organic matter

Soil organic matter obeys the following,

$$\frac{\partial C_{s,k}}{\partial t} = (1 - f_{\text{resp}}) P_k \sum_{j=1}^3 k_{l,j} C_{l,j} - k_{s,k} C_{s,k}, \quad (15)$$

where k is an index for the fast ($k = 1$) and slow ($k = 2$) soil carbon pools, $C_{s,k}$ is soil organic carbon to 1 m depth and $k_{s,k}$ is the decomposition constant. The fraction of the decomposed litter

carbon lost to the atmosphere as CO_2 is represented by f_{resp} (Table 1) and is estimated to be approximately 0.70, with some variation between biomes (Parton et al., 1987; Parton et al., 1992). The variations in the microbial respiration fraction reflect variations in litter quality, lignin content and the soil texture that are associated with these biomes (Parton et al., 1992). The remaining carbon, $(1 - f_{\text{resp}})$, represents the amount of litter carbon that becomes soil organic matter.

The turnover times ($1/k$) for the fast and slow soil organic matter pools, at 20°C and ample soil moisture, are 15 and 750 years, respectively. These values were selected by reviewing soil carbon budget analyses and radiocarbon dating studies presented in the literature (Jenkinson, 1977; Parton et al., 1987; Jenkinson, 1990; Anderson, 1992; Raich and Schlesinger, 1992). The values for pool turnover times in this model are similar to the values used in multi-compartment soil carbon models of Parton et al. (1987, 1992) and Jenkinson (1990).

The partitioning coefficients for carbon flowing into the fast and slow soil pools, P_1 and P_2 , are 0.985 and 0.015 respectively (see Table 1). These parameters are globally fixed, with two exceptions: tropical rainforests and tropical seasonal forests are assumed to have $P_1 = 0.980$ and $P_2 = 0.020$. The changes in P_k reflect the effects of changes in soil texture associated with the different biomes (Parton et al., 1992). In reality humus fractions are distributed through a continuum of turnover times. However, for the purposes of simulating the global-scale patterns of equilibrium soil carbon storage, a two compartment model should be sufficient (Jenkinson, 1990; Parton et al., 1992).

Under equilibrium conditions the time derivative in eq. (15) falls out, leaving,

$$C_{s,k} = \frac{(1 - f_{\text{resp}}) P_k \sum_{j=1}^3 k_{l,j} C_{l,j}}{k_{s,k}}. \quad (16)$$

Parton et al., (1987, 1992) and Jenkinson (1990) have used simple relationships between the decomposition rate, temperature and soil moisture. In DEMETER, the control of climate in the turnover of soil carbon is expressed by,

$$k_{s,k} = k_{s0,k} f(T) g(M), \quad (17)$$

where $k_{s0,k}$ represents the turnover rate of soil carbon pools at 20°C and ample soil moisture, and

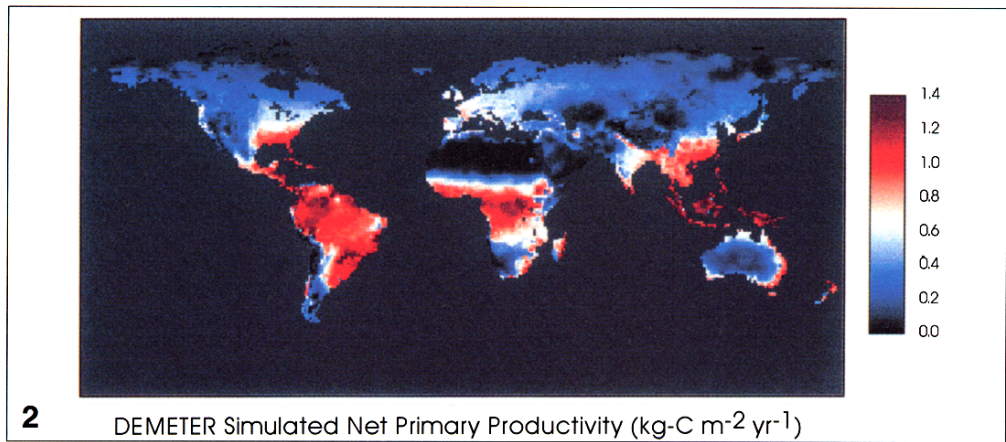


Fig. 2. Net primary productivity (NPP) for the modern climate as simulated by DEMETER-1 (Foley, 1994).

$f(T)$ and $g(M)$ are functions of the annual mean air temperature and soil moisture, respectively, soil moisture and M_{sat} is the saturated soil moisture.

$$f(T) = \exp\left(\frac{\ln(Q_{10,\text{soil}})}{10}(T - 20)\right), \tag{18}$$

$$g(M) = 0.25 + 0.75\left(\frac{M}{M_{\text{sat}}}\right), \tag{19}$$

where $Q_{10,\text{soil}}$ is a temperature sensitivity parameter for soil respiration (fixed to 2.0), M is

3. Results

The simulations of the terrestrial carbon budget are compared to observations and previous modeling studies. There are several global datasets describing the state of the terrestrial vegetation (Matthews, 1983; Olson et al., 1983), NPP (Lieth

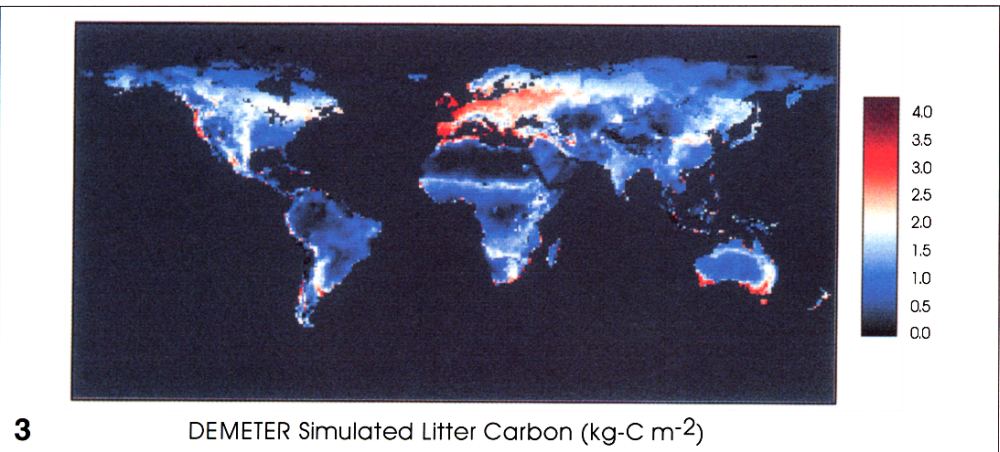


Fig. 3. Carbon in litter as simulated by DEMETER-1.

and Whittaker, 1975; Atjay et al., 1979; Raich et al., 1991; McGuire et al., 1992), litter carbon (Schlesinger, 1977), and soil carbon (Schlesinger, 1977; Post et al., 1982; Zinke et al., 1984).

Foley (1994) presents a more complete discussion of the NPP simulation and its validation; here only the general results are mentioned. Patterns of simulated NPP (Fig. 2) are strongly correlated to field observations ($r=0.9343$) and the results of the empirically-based Miami Model (Lieth, 1975) ($r=0.9587$). Global NPP (Table 3) is simulated to be 62 Gt-C yr^{-1} , which is comparable to previous estimates (45 to 70 Gt-C yr^{-1}) (Whittaker and Likens, 1973; Lieth and Whittaker, 1975; Atjay et al., 1979). The tropical biomes (tropical rainforest, tropical seasonal forest and tropical dry forest/savanna) contribute the largest fraction of the global NPP (Table 3).

Global vegetation carbon is simulated to be 800 Gt-C (Table 3), which is comparable to previous estimates (Whittaker and Likens, 1973; Atjay et al., 1979; Olson et al., 1983). Tropical rainforest and tropical seasonal forests have the most vegetation carbon (134 and 110 Gt-C , respectively), followed by the boreal forests (100 Gt-C) (Table 3).

Global litter carbon is simulated to be 150 Gt-C

(Table 3). This result is well within the range of previous estimates (55 Gt-C by Schlesinger, 1977) and other modeling studies (210 Gt-C by Esser et al., 1982). The boreal forest biome contains the most litter carbon (18.69 Gt-C) (Table 3). Litter carbon represents a substantial fraction (simulated here as 6%) of the terrestrial carbon budget; however, published estimates of the size of this reservoir vary by a factor of 4.

The spatial distribution of litter carbon density is presented in Fig. 3. Note that the amount of litter carbon is achieved by a balance between litterfall and decomposition. Litter carbon density is a maximum in the cool mixed forests (2.06 kg-C m^{-2}), and is a minimum in tropical rainforests (0.44 kg-C m^{-2}) and deserts (0.59 kg-C m^{-2}) (Table 2).

Global soil organic matter to 1 m is simulated to $1,373.0 \text{ Gt-C}$ (Table 3), which is within the range of other estimates ($1,456 \text{ Gt-C}$ by Schlesinger, 1977; $1,395 \text{ Gt-C}$ by Post et al., 1982; $1,309 \text{ Gt-C}$ by Zinke et al., 1984; $1,457 \text{ Gt-C}$ by Meentemeyer et al., 1985; 1220 Gt-C by Sombroek et al., 1993). The expansive boreal forest contains the most soil carbon (200.2 Gt-C), followed by tundra (185.6 Gt-C) (Table 3).

Simulated soil carbon density is presented

Table 2. Simulated NPP and carbon storage densities

	Biome name	Biome area 10^{13} m^2	NPP ($\text{kg-C m}^{-2} \text{ yr}^{-1}$)	Vegetation carbon (kg-C m^{-2})	Litter carbon (kg-C m^{-2})	Soil carbon (kg-C m^{-2})
1	tropical rainforest	0.6273	1.20	20.0	0.44	10.17
2	tropical seasonal forest	0.7900	1.03	14.0	0.61	10.63
3	tropical dry forest & savanna	1.6420	0.79	4.5	1.04	7.82
4	warm mixed forest	0.7832	0.94	10.0	1.54	13.68
5	temperate deciduous forest	0.6420	0.59	10.0	1.82	13.20
6	cool mixed forest	0.5388	0.51	10.0	2.06	14.99
7	cool conifer forest	0.3717	0.38	17.0	1.95	15.92
8	boreal forest	1.2370	0.29	8.2	1.51	16.18
9	cold mixed forest	0.0919	0.36	10.0	1.79	16.08
10	cold deciduous forest	0.3021	0.19	7.9	0.98	17.66
11	xerophytic woods & scrub	1.0360	0.50	4.0	1.83	8.41
12	warm grass & shrub	1.0650	0.25	1.5	1.23	8.03
13	cool grass & shrub	0.4240	0.26	1.0	1.28	17.95
14	tundra	1.2340	0.16	1.2	0.80	15.04
15	hot desert	1.7600	0.10	0.5	0.59	1.96
16	semidesert	0.3810	0.12	0.5	0.68	6.08
17	ice & polar desert	0.2282	0.00	0.0	0.00	0.00
	Global average		0.47	6.0	1.14	10.40

Table 3. *Simulated NPP and carbon storage*

	Biome name	NPP (Gt-C/yr)	Vegetation carbon (Gt-C)	Litter carbon (Gt-C)	Soil carbon (Gt-C)
1	tropical rainforest	8.1	134.5	3.0	68.4
2	tropical seasonal forest	8.2	110.6	4.8	84.0
3	tropical dry forest & savanna	13.0	73.9	17.1	128.5
4	warm mixed forest	7.4	78.3	12.0	107.1
5	temperate deciduous forest	3.8	64.2	11.7	84.8
6	cool mixed forest	2.7	53.9	11.1	80.8
7	cool conifer forest	1.4	63.2	7.3	59.2
8	boreal forest	3.5	100.9	18.7	200.2
9	cold mixed forest	0.3	9.2	1.6	14.8
10	cold deciduous forest	0.6	24.0	3.0	53.4
11	xerophytic woods & scrub	5.1	41.4	19.0	87.1
12	warm grass & shrub	2.6	16.0	13.1	85.5
13	cool grass & shrub	1.2	4.2	5.4	76.1
14	tundra	2.0	15.2	9.9	185.6
15	hot desert	1.8	8.8	10.4	34.5
16	semidesert	0.4	1.9	2.6	23.2
17	ice & polar desert	0.0	0.0	0.0	0.0
	global total	62.1	800.2	150.7	1373.2

in Fig. 4. Boreal forests and tundra have high simulated soil carbon densities (15.9 and 17.6 kg-C m⁻²) (Table 2), while deserts and tropical grasslands have low densities (1.9 and 7.8 kg-C m⁻²). Simulated biome-average soil carbon densities are in strong agreement with the soil

carbon data presented by Post et al. (1982) and Zinke et al. (1984) (Table 4). A linear regression between the simulated and observed biome-average soil carbon densities yields a correlation coefficient, *r*, of 0.9373 (Fig. 5). However, there is more variation between individual gridcells

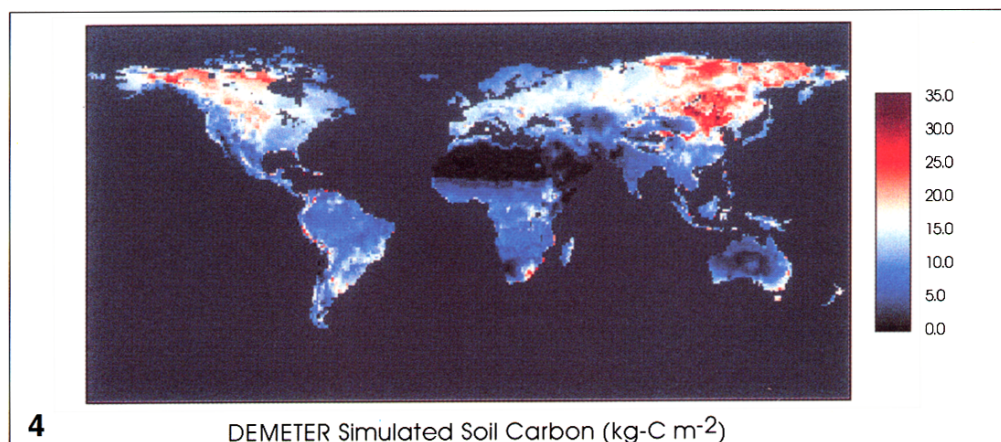


Fig. 4. Carbon in soil organic matter as simulated by DEMETER-1.

Table 4. Comparisons between the simulated biome-average soil organic matter densities (to 1 m depth) and observations (Post et al., 1982; Zinke et al., 1984)

	Biome name	DEMETER soil carbon (kg-C m ⁻²)	Zinke et al. soil carbon (kg-C m ⁻²)
1	tropical rainforest	10.2	10.5
2	tropical seasonal forest	10.6	10.5
3	tropical dry forest & savanna	7.8	7.5
4	warm mixed forest	13.7	13.5
5	temperate deciduous forest	13.2	15.0
6	cool mixed forest	15.0	13.0
7	cool conifer forest	15.9	15.0
8	boreal forest	16.2	15.8
9	cold mixed forest	16.1	13.0
10	cold deciduous forest	17.7	15.5
11	xerophytic woods & scrub	8.4	7.5
12	warm grass & shrub	8.0	9.0
13	cool grass & shrub	18.0	12.5
14	tundra	15.0	17.7
15	hot desert	2.0	3.0
16	semidesert	6.1	6.0
17	ice & polar desert	0.0	0.0
	Global average	10.4	10.4

(Fig. 6). The simulated patterns of soil carbon density (Fig. 4) are in good agreement with previous studies (Schlesinger, 1977; Kadeba, 1978; Sanchez et al., 1982; Sombroek et al., 1993).

4. Discussion

This manuscript presents a simulation of the equilibrium terrestrial carbon budget. The model

simulates the global total carbon storage potential of vegetation (800.1 Gt-C), litter (150.4 Gt-C) and soil (1,373.0 Gt-C). These results fall within the ranges of previous estimates (Whittaker and Likens, 1973; Schlesinger, 1977; Atjay et al., 1979; Post et al., 1982; Olson et al., 1983; Zinke et al., 1984). Global-scale patterns of carbon fluxes and reservoirs are in good agreement with previous studies. In particular, the biome-average

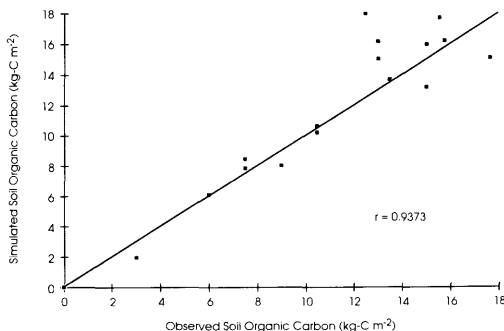


Fig. 5. Correlation between biome-average soil carbon density simulations and observations (Post et al., 1982; Zinke et al., 1984).

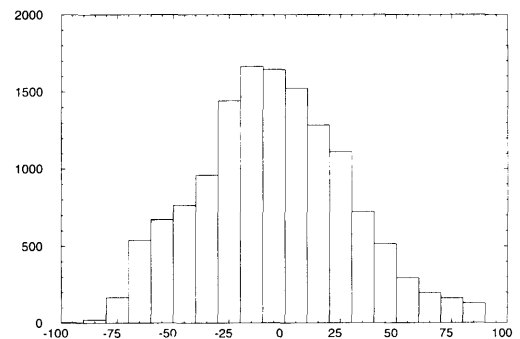


Fig. 6. Histogram of differences (%) between DEMETER-1 simulated soil carbon densities and biome-average observations (Post et al., 1982; Zinke et al., 1984).

soil carbon densities are in strong agreement ($r = 0.9373$) with soil carbon density observations (Post et al., 1982; Zinke et al., 1984).

DEMETER-1 is designed to provide a global-scale view of the terrestrial carbon budget and its possible sensitivity to climatic change. However, this first version of the model is highly simplified and does not include many important ecosystem processes. For example, the role of mineral nutrients, soil parent material and soil texture are not explicitly represented by the model. Nevertheless, the model appears to reproduce the global-scale patterns observed in the terrestrial biosphere.

DEMETER-1 is one of several process-based terrestrial biosphere models available today (Raich et al., 1991; McGuire et al., 1992; Melillo et al., 1993; Potter et al., 1993). One major difference between DEMETER and many of the other models is that DEMETER does not consider mineral nutrients. Simulating the complex interactions between carbon and mineral nutrients requires a large number of parameters that must be tuned or calibrated. It is possible that the tuning and calibration process gives rise to unrealistic

parameter choices, which may affect the model's sensitivity to environmental change. Using a simpler process-based model at the outset may avoid these potential problems. Future versions of DEMETER will gradually add more complexity and realism, assuming that the additional processes are fully understood and can be validated.

5. Acknowledgments

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