Tellus (1995), 47B, 501–519
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TELLUS
ISSN 0280–6509

In search of the missing carbon sink: a model of terrestrial biospheric response to land-use change and atmospheric CO_2

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(Manuscript received 20 June 1994; in final form 6 March 1995)

ABSTRACT

Estimates of the net exchange of carbon between the terrestrial biosphere and the atmosphere may be too large because the models of carbon release from changes in land use do not allow for enhanced carbon assimilation by the terrestrial biosphere in response to increasing atmospheric CO_2. We address this deficiency with a model of terrestrial biosphere that includes both ecosystem response to land-use perturbation and vegetation response to atmospheric CO_2. Model inputs specify the areas affected by land-use change since 1700. The carbon dynamics of the affected areas are described by an area distribution function for vegetation carbon density and a compartment model of carbon in vegetation, litter, and soil. Vegetation growth is modeled as the difference between net primary production (NPP) and mortality. NPP, the net flux of carbon from atmosphere to vegetation, is a logistic function of vegetation carbon density. The response of NPP to atmospheric CO_2 is modeled with three response functions: a logarithmic, a rectangular-hyperbolic, and a response function derived from a biochemical model of C_3 photosynthesis. The response functions are parameterized by ecosystem type with data from CO_2 exposure experiments. Elevated CO_2 affects the NPP of both undisturbed and recovering ecosystems. We use the model to test the hypothesis that the CO_2 enhancement of terrestrial NPP explains the historical missing carbon sink of the global carbon cycle budget. Our estimates of the biosphere's CO_2 enhanced carbon flux are much smaller than the reconstructed missing carbon sink. We conclude that our model results do not support the hypothesis.

1. Introduction

When terrestrial ecosystems are disturbed by deforestation and other changes in land use they release CO_2 to the atmosphere. The combination of CO_2 emissions from land-use change with those from fossil fuel combustion and cement manufacturing is widely accepted as the primary source of the increase in atmospheric CO_2 recorded for the industrial era (ca. 1700-present) (Houghton et al., 1990; 1992). Histories of both land-use and industrial CO_2 emissions are essential in the simulation of past, present, and future changes in atmospheric CO_2.

Industrial CO_2 emissions are reconstructed from data on fossil fuel and cement production using formulas that translate the production data into the CO_2 releases associated with utilization (Marland et al., 1989). The history generated by Marland et al. (1989 and later revisions) is widely accepted as one of the better known components of the global carbon cycle with uncertainties estimated at about $\pm 10\%$ (Marland et al., 1989; Houghton et al., 1992). The history of land-use CO_2 emissions is much less certain.

The most direct estimates of historical CO_2 emissions from land-use change come from models

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that explicitly simulate the disturbance of terrestrial ecosystems by deforestation and other changes in land-use (Houghton et al., 1983; Rotmans and Swart, 1991; Emanuel et al., 1993). These models are driven by historical data on the areas and rates of global land-use change. They track the long-term fate of carbon in, and removed from, the disturbed ecosystems and produce an estimate of the net exchange of CO_2 between the atmosphere and the terrestrial biosphere. Estimates from these models are highly uncertain, on the order of $\pm 60\%$ (Houghton et al., 1992), because of uncertainties in: (1) areas and rates of land-use change, (2) estimates of ecosystem biomass prior to land-use change, and (3) the understanding of the fate of ecosystem carbon following disturbance. Furthermore, the emission histories they generate are consistently incompatible with nearly all contemporary models of carbon uptake by the world's oceans (Enting and Mansbridge, 1987; King et al., 1992; Rotmans and Den Elzen, 1993). When the histories of CO_2 emissions from the land-use emissions models are combined with the history of industrial CO_2 emissions from Marland et al. (1989), the global ocean-atmosphere carbon cycle models tend to overestimate observed atmospheric CO_2 concentrations and rates of change.

Compatible histories of the net biosphere-atmosphere exchange can be estimated using models of carbon exchange between the atmosphere and the oceans to deconvolve the historical record of atmospheric CO_2 or carbon isotopes (Siegenthaler and Oeschger, 1987; Keeling et al., 1989; King et al., 1991; Wigley, 1991; Sarmiento et al., 1992). The residual non-fossil flux generated by the deconvolution is often attributed to the terrestrial biosphere. These analyses suggest that the terrestrial biosphere was a nearly constant or slightly increasing net CO_2 source during the 19th Century. The source estimated by deconvolution begins to decline in the late 19th or early 20th Century, and most analyses suggest that the terrestrial biosphere switched from a net source to a net sink in about 1940–1950. The sink increased to a maximum during the 1970s and then began to weaken. Many of the deconvolutions suggest that the terrestrial biosphere again became a small net source in the early 1980s.

In contrast, land-use emissions models characteristically generate a net biospheric source that increases almost continuously during the 19th and 20th Centuries (Houghton et al., 1983; Houghton and Woodwell, 1989; Houghton and Skole, 1990; Houghton, 1991a, b; Rotmans and Swart, 1991; Emanuel et al., 1993; IPCC, 1993). The deconvolutions predict a slowly declining source for the early to mid-20th Century. For this same period the land-use emissions models predict a rapidly increasing source. For the 1970s, the land-use models predict a nearly constant or slightly declining source while the deconvolutions predict a maximum sink in that decade. The simulated land-use emissions source increases again to a maximum in the late 1980s (Houghton 1991a, b).

The differences between the estimates by deconvolution and those from the land-use emissions models represent an imbalance in the global carbon budget, a "missing sink". Estimates of the missing sink for the decade 1980–1989 are as high as 1.6 ± 1.4 Gt C yr^{-1} (Houghton et al., 1990; 1992). A variety of hypotheses have been suggested as possible explanations of the missing carbon sink. Foremost is the idea that elevated concentrations of atmospheric CO_2 have enhanced photosynthetic uptake and storage of carbon by terrestrial ecosystems.

Most land-use emissions models do not explicitly include vegetation response to atmospheric CO_2 (the model of Rotmans and Den Elzen [1993] is an exception), and thus a potentially important process in the global carbon cycle may be missing from the modeled carbon budgets. Here we describe a model of the terrestrial biosphere as part of the global carbon cycle that explicitly includes both ecosystem response to land-use perturbation and vegetation response to atmospheric CO_2. We use the model to test the hypothesis that CO_2 fertilization of the terrestrial biosphere explains the missing carbon sink.

2. The model

2.1. General structure and land-use change

An earlier version of the model, which did not include vegetation response to atmospheric CO_2, has been described elsewhere (Emanuel et al., 1993; King et al., 1994). The earth's land surface is divided into 10 continental regions and 13 biomes (Table 1). Carbon in each biome of each region is

Table 1. *Biome areas (10^{12} m^2) in 1700 within regions of the world*

Biome	North America	Europe	FSU†	Developed Pacific	China	Latin America	North Africa Middle East	Tropical Africa	South Asia	Southeast Asia
tropical moist forest				1.66	0.14	5.00	0.19	4.26	0.12	2.15
tropical seasonal forest						1.75		4.81	1.34	0.38
temperate evergreen forest	2.36	0.85	1.08	0.32	0.40	0.26	0.19			
temperate deciduous forest	1.57	0.65	1.48	0.49	0.81	1.12				
boreal forest	3.94	0.35	7.50							
tropical woodland				0.20		2.85		4.51	1.89	
temperate woodland	2.29	0.45	1.32			3.47				
tropical grassland				4.97		0.74	0.90	4.59	1.82	1.23
temperate grassland	5.68	0.88	1.75		7.23	4.97				
tundra and alpine meadow	3.43	0.27	3.36							
desert scrub			5.04	1.18	1.45		9.79	4.06		
cultivated land	0.03	0.67	0.33	0.05	0.29	0.07	0.20	0.44	0.53	0.04
pasture land	0.04	0.75	0.53	0.24	0.83	0.37	0.54	1.87	0.07	0.02
total	19.34	4.87	22.39	9.11	11.15	20.60	11.81	24.54	5.77	3.82

Data are from Houghton et al. (1983).
† Former Soviet Union (USSR).

divided among three reservoirs: live vegetation, litter, and soil (Fig. 1). The vegetation carbon density per unit of land area c_v of each biome within each region is described by an area distribution function $A(c_v, t)$, which specifies the area at time t with carbon density c_v. Details of the area distribution function can be found in Emanuel et al. (1993) and Emanuel (1995). The total vegetation carbon is

$$C_v = \int_0^{c_{max}} cA(c, t)\, dc, \tag{1}$$

where c_{max} is the maximum vegetation carbon density. The mean vegetation carbon density $\bar{c}_v$ is

$$\bar{c}_v = C_v / A_T, \tag{2}$$

where A_T is the total area of the biome within the region:

$$A_T = \int_0^{c_{max}} A(c_v, t)\, dc_v. \tag{3}$$

We assume an initial equilibrium preagricultural condition in which all vegetation is at maximum density c_{max}. We treat litter and soil carbon pools as well-mixed carbon reservoirs with carbon densities c_l and c_s, respectively. Our estimates of initial equilibrium terrestrial biosphere carbon storage are given in Table 2.

Plant growth increases vegetation carbon density, moving area in the distribution $A(c_v, t)$ from lower to higher densities. Plant mortality decreases vegetation carbon density and moves area in $A(c_v, t)$ to lower densities. The dynamics of the area distribution of vegetation carbon density in each biome within each region are described by:

$$\frac{\partial}{\partial t} A(c_v, t) + \frac{\partial}{\partial c}\left(g(c_v, t)\, A(c_v, t)\right) = 0, \tag{4}$$

where $g(c_v, t)$ is a general function describing the rate of change of vegetation carbon density. The change in vegetation density is the difference between net primary production (NPP) and losses through litterfall, mortality, and herbivore consumption:

$$g(c_v, t) = P_n - L, \tag{5}$$

where P_n is NPP, and L is litter production (combining losses to litterfall, mortality, and herbivore consumption).

NPP is the difference between gross carbon uptake by photosynthetic assimilation and return to the atmosphere by autotrophic respiration. Experimentally, C_3 plant species generally respond to elevated concentrations of ambient CO_2 with higher rates of photosynthesis and growth. We assume that, through CO_2 stimulation of photosynthesis, concentrations of atmospheric CO_2 above preindustrial levels increase NPP in terrestrial vegetation. We also assume that NPP varies with biomass carbon according to a logistic plant growth equation. Thus,

$$P_n = (vc_v - \rho c_v^2)\, r(p_a), \tag{6}$$

where $r(p_a)$ expresses the dependence of NPP on atmospheric CO_2 concentration p_a, v is an intrinsic growth rate, and ρ determines the asymptotic level to which vegetation carbon density converges. Our model simply assumes that NPP (and thus plant growth through eq. (5)) is dependent on atmospheric CO_2, an assumption common to many global carbon cycle models. We make no attempt to resolve the mechanism of this dependency. For example, our model implicitly assumes a uniform increase in growth rate over all canopy sizes. Alternatively, the major effect of increased CO_2 could be an increase in maximum canopy size (proportional to our c_{max}) as photosynthesis in the light limited portion of the canopy responded disproportionally to elevated CO_2

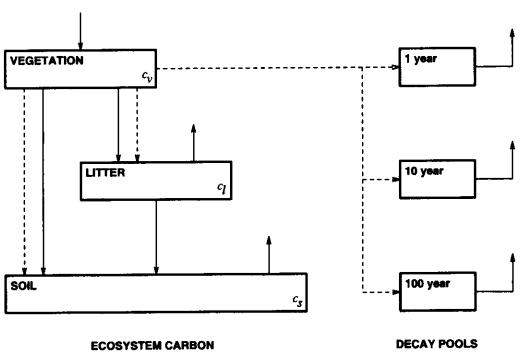

Fig. 1. A compartment representation of carbon in terrestrial ecosystems. The dashed lines represent transfers of carbon that accompany changes in land use. The turnover times of the decay pools are from Houghton et al. (1983).

Table 2. *Terrestrial net primary production and carbon storage in 1700*

Biome	Net primary production ($kg\ C\ m^{-2}\ yr^{-1}$)	Net annual production ($Gt\ C\ yr^{-1}$)	Vegetation carbon density ($kg\ m^{-2}$)	Carbon in vegetation (Gt)	Litter carbon density ($kg\ m^{-2}$)	Carbon in litter (Gt)	Soil carbon density ($kg\ m^{-2}$)	Carbon in soil (Gt)
tropical moist forest	0.900	12.17	20.0	270.4	0.2	2.7	11.5	155.5
tropical seasonal forest	0.675	5.59	16.0	132.5	0.2	1.7	11.5	95.2
temperate evergreen forest	0.585	3.19	16.0	87.4	1.4	7.6	12.0	65.5
temperate deciduous forest	0.540	3.30	13.5	82.6	1.4	8.6	12.0	73.4
boreal forest	0.360	4.24	9.0	106.1	2.8	33.0	17.8	209.9
tropical woodland/shrubland	0.270	2.55	2.7	25.5	0.3	2.8	6.6	62.4
temperate woodland/shrubland	0.270	2.03	2.7	20.3	0.3	2.3	6.6	49.7
tropical grassland	0.315	4.49	1.8	25.7	0.1	1.4	4.1	58.4
temperate grassland	0.225	4.61	0.7	14.4	0.2	4.1	18.7	383.5
tundra and alpine meadow	0.065	0.46	0.3	2.1	0.5	3.5	19.9	140.5
desert scrub	0.032	0.69	0.3	6.5	0.01	0.2	5.8	124.6
cultivated land	0.290	0.77	0.5	1.3	0.03	0.1	7.9	20.9
pasture land	0.225	1.53	0.7	3.7	0.2	1.1	18.7	98.4
total		46.05	778.4		69.1		1537.9	

Biome areas used to calculate biome production and carbon storage are from Table 1. Estimates of net primary production are from Whittaker and Likens (1973). Vegetation and litter plus soil carbon densities are from Houghton et al. (1983). Partitioning between litter and soil is from Schlesinger (1977).

(McMurtrie et al., 1992). In initializing eq. (6), we assume an equilibrium condition in which $r(pa) = 1.0$ and $c_v = c_{max}$ (Table 2). Our estimates of initial equilibrium NPP are in Table 2.

The production flux P_n is the net flux of carbon from the atmosphere to live vegetation f_{av}. The loss term L is the sum of the fluxes from vegetation to litter and soil f_{vl} and f_{vs}, respectively. The rate of change in vegetation carbon density is then

$$g(c_v, t) = f_{av} - f_{vl} - f_{vs}. \tag{7}$$

The litter fluxes are linearly proportional to vegetation carbon density. The equation describing changes in vegetation carbon density on an elemental land unit is

$$\frac{dc_v}{dt} = (vc_v - \rho c_v^2)\, r(p_a) - (\alpha_{vl} + \alpha_{vs})\, c_v. \tag{8}$$

Eq. (8) substitutes for $g(c_v, t)$ in eq. (4).

The transfer of litter carbon to soil carbon and the fluxes of carbon to the atmosphere from the litter and soil carbon pools (Fig. 1) are modeled as first-order donor-controlled processes. Changes in litter and soil carbon are described by:

$$\frac{dc_l}{dt} = \alpha_{vl}\bar{c}_v - (\alpha_{ls} + \alpha_{la})\, c_l, \tag{9}$$

$$\frac{dc_s}{dt} = \alpha_{vs}\bar{c}_v + \alpha_{ls} c_l - \alpha_{sa} c_s, \tag{10}$$

where c_l and c_s are litter and soil carbon densities, respectively.

Changes in land use transfer carbon from vegetation to litter and soil (Fig. 1) and alter the area distribution of vegetation carbon. The carbon added to litter and soil pools decays according to the turnover dynamics of each reservoir, and carbon is released to the atmosphere. Changes in land use also transfer carbon from vegetation to decay pools (Fig. 1) that model the fate of plant material burned on site as part of the land-use disturbance and the fate of wood products removed from the site. Decay from these pools also releases carbon to the atmosphere. There are three decay pools with turnover times of 1, 10, and 100 years. The 1-year turnover pool models burning during the land-use disturbance and the oxidation of fuelwood. The decay of paper products is described by the 10 year turnover pool, and the 100-year turnover pool models the decay of industrial lumber or other long-lived products (Houghton et al., 1983; Houghton, 1993). Losses to the atmosphere from the decay pools are linearly proportional to their contents:

$$\frac{dc_j}{dt} = -\frac{c_j}{\tau_j} + \sum_{i=1}^{n} f_{ij}^{d}(t), \tag{11}$$

where c_j is the carbon content of the jth decay pool ($j = 1, 2, 3$), and τ_j is the time constant for that pool (1, 10, and 100 years, respectively). The carbon flux f_{ij}^{d} is the input into decay pool j from land-use forcing i, and n is the number of land-use forcings.

We currently consider three types of land-use change: (1) the clearing of natural ecosystems for cropland, (2) recovery of cropland to pre-conversion natural vegetation following abandonment of agricultural land, and (3) the harvest of forest ecosystems for wood products. These disturbances are modeled as forcing functions applied to eq. (4):

$$\frac{\partial}{\partial t} A(c_v, t) + \frac{\partial}{\partial c}\left(g(c_v, t)\, A(c_v, t)\right) = \sum_{i=1}^{n} z_i(c_v, t), \tag{12}$$

where $z_i(c_v, t)$ is the ith land-use forcing function in units of area per unit time as a function of carbon density and time, and n is the number of kinds of land-use change applied.

Clearing for cropland $z_c(c_v, t)$ removes area from the disturbed biome's area distribution function and transfers it (i.e., adds it) to the cropland area of the affected region. The area of the natural biome within that region is reduced, and the area of cropland is increased by the same amount. Area is removed at a specific carbon density in proportion to the area at that density:

$$z_c(c_v, t) = -z_c'(t)\,\frac{A(c_v, t)}{A_T}, \tag{13}$$

where $z_c'(t)$ is the total area cleared at time t, and A_T is the total area of the biome within the region (eq. (3)).

A third of the carbon removed from natural vegetation by clearing for agriculture is transferred to the biome's litter compartment. The remaining two-thirds is distributed among the three decay

pools. We use the fractions assigned to decay pools after clearing in Table 3 of Houghton et al. (1983).

When cropland is abandoned, the area $z'_a(t)$ is returned to the area distribution for the natural biome at an initial minimum carbon density c_{min}:

$$z_a(c_v, t) = \begin{cases} z'_a(t) & \text{if } c_v = c_{min}, \\ 0 & \text{otherwise.} \end{cases} \quad (14)$$

The vegetation recovers from c_{min} according to the logistic growth function of eq. (8), and the area distribution of carbon density shifts toward maximum carbon density.

Forest harvest does not change the area of the forested biome, transferring area at a specific carbon density in proportion to the area at that density to area at minimum carbon density:

$$z_h(c_v, t) = \begin{cases} -z'_h(t) & \text{if } c_v > c_{min}, \\ z'_h(t) & \text{if } c_v = c_{min}, \\ 0 & \text{otherwise.} \end{cases} \quad (15)$$

Only a fraction of the vegetation carbon in the harvested area is removed as harvested wood product (approximately 22% from primary tropical moist forest or 13% from primary boreal forest, Houghton et al., 1983). Harvested carbon is distributed among the three decay pools of eq. (11). We use the fractions of roundwood (i.e., timber) assigned to decay pools from Appendix 2 in Houghton et al. (1983). These fractions vary through time and between regions. Most of the vegetation carbon in the harvested area is transferred to the biome's litter and soil pools as dead plant material (approximately 79% in primary tropical moist forest).

Harvested forest recovers to c_{max} according to the logistic growth equation eq. (8). During this recovery, and the recovery of abandoned cropland, carbon is transferred from the atmosphere to the vegetation by NPP. The net annual exchange with the atmosphere for any year following the harvest event is the difference between this carbon uptake and the release to the atmosphere from decay in the biome's litter and soil carbon pools and the three extra-biome decay pools.

Numerical solution of the system of equations eqs. (9)–(12) for each biome in each continental region gives the net annual flux of carbon between the atmosphere and each bioregion. The global annual net flux is the sum of the annual net fluxes for each biome in each continental region.

2.2. CO_2 enhancement of NPP

We consider three alternative formulations of the CO_2 response function $r(p_a)$ expressing the dependence of NPP on atmospheric CO_2 (eq. (6)). The first is the frequently used logarithmic function of Keeling (1973) (also Bacastow and Keeling, 1973):

$$r_1(p_a) = 1 + \beta_1 \ln\left(\frac{p_a}{p_a^0}\right), \quad (16)$$

where p_a^0 is the equilibrium preindustrial CO_2 concentration, and β_1, often referred to as the biotic growth factor, is a constant, which may vary with vegetation type but does not itself change with atmospheric CO_2.

The logarithmic function of eq. (16) has been criticized as a poor representation of C_3 plants' physiological response to elevated CO_2 (Gifford, 1980; Gates, 1985). A rectangular-hyperbolic function has been suggested as a more appropriate representation (Gifford, 1980; Allen et al., 1987). However, we want to be able to compare any response derived from physiological considerations with those from the commonly used biotic growth factor formulation of eq. (16). Therefore, we define a second CO_2 response function:

$$r_2(p_a) = 1 + \beta_2 \frac{p_a - p_a^0}{p_a^0}, \quad (17)$$

where β_2 is the biotic growth factor derived by Allen et al. (1987) for a modified rectangular-hyperbola model of photosynthetic response to CO_2. The modified rectangular hyperbola is like the Michaelis-Menten equation of enzyme kinetics and takes the form:

$$R = \frac{R_m p_a}{p_a + K_m} + R_i, \quad (18)$$

where R is photosynthesis (or any other response), p_a is ambient atmospheric CO_2 concentration, R_i is the y-axis intercept for R, R_m is the asymptotic response limit of $(R - R_i)$ at high p_a, and K_m is the

p_a at which $(R - R_i) = 0.5R_m$ (Allen et al., 1987). The biotic growth factor is defined by

$$\beta_2 = \frac{\partial R}{\partial p_a}\frac{p_a}{R}, \tag{19}$$

or:

$$\beta_2 = \frac{K_m}{p_a + K_m}\frac{R_m p_a}{R_m p_a + R_i(p_a + K_m)} \tag{20}$$

(Allen et al., 1987). β_2 is thus an explicit function of atmospheric CO_2 with three parameters: R_m, R_i, and K_m.

The currently most accepted model of C_3 photosynthesis is the biochemical model of Farquhar and von Caemmerer (1982). Polglase and Wang (1992) derived a biotic growth factor for leaf photosynthesis from this model with a few simple assumptions. If dark respiration is proportional to leaf photosynthesis (Polglase and Wang, 1992),

$$\beta_3 = \frac{3\chi p_a \Gamma^*}{(\chi p_a - \Gamma^*)(\chi p_a + 2\Gamma^*)}, \tag{21}$$

where $\chi = p_i/p_a$, p_i is the internal (intercellular) CO_2 concentration, and Γ^* is the CO_2 compensation point in the absence of day respiration. Γ^* for C_3 plants is a function of temperature (T, °C):

$$\Gamma^* = 42.7 + 1.68(T - 25) + 0.012(T - 25)^2. \tag{22}$$

We thus define a third CO_2 response function:

$$r_3(p_a) = 1 + \beta_3 \frac{p_a - p_a^0}{p_a^0}. \tag{23}$$

Note that β_3 like β_2 is a decreasing function of atmospheric CO_2. β_3 is also a function of temperature, with the rate of change in β_3 as a function of CO_2 increasing with higher temperatures (Polglase and Wang, 1992).

As first formulated and used in early applications, β_1 of eq. (16) was adjusted to match changes in atmospheric CO_2 generated by a global carbon cycle model with CO_2 observations from Mauna Loa Observatory, Hawaii (Bacastow and Keeling, 1973). Subsequently, there have been efforts to quantify β_1 from experimental studies of plants exposed to elevated CO_2 (Gifford, 1980; Kohlmaier et al., 1981; Kohlmaier et al., 1987; Allen et al., 1987). The definitions of β_2 and β_3 used above arose from these efforts. The translation from experimental photosynthesis or plant growth results to a large-scale parameter applied

Table 3. *CO_2 response parameters determined from experimental results*

Biome	β_{E_1}	R_m	R_i	K_m (ppmv)	β_{E_2}
tropical moist forest	0.54	3.61	−0.39	566	0.58
tropical seasonal forest	0.67	3.39	−0.35	519	0.54
temperate evergreen forest	0.57	3.39	−0.18	721	0.52
temperate deciduous forest	0.71	3.35	−0.57	392	0.58
boreal forest	0.56	2.82	−1.00	141	0.42
tropical woodland and shrubland	0.67	2.85	−0.82	199	0.48
temperate woodland and shrubland	0.59	3.16	−0.51	384	0.55
tropical grassland	0.21	1.85	−0.78	14	0.05
temperate grassland	0.31	2.18	−0.77	82	0.24
tundra and alpine meadow	0.81	3.66	−0.72	394	0.65
desert scrub	0.60	2.65	−0.55	250	0.45
cultivated land	0.57	2.73	−0.43	328	0.48
pasture land	0.66	2.88	−0.76	227	0.50

The parameters β_{E_1} and β_{E_2} are experimentally determined biotic growth factors for photosynthetic response to elevated CO_2 described by logarithmic and rectangular-hyperbolic functions, respectively. The parameters R_m, R_i, and K_m define the shape of the rectangular hyperbola from which β_{E_2} is derived (see eqs. (18) and (20) in the text). The response factor β_{E_2}, a function of CO_2 concentration, is calculated for an initial atmospheric CO_2 concentration of 276.8 ppmv.

to global or biome NPP involves many assumptions, many of them tenuous, and the legitimacy of the effort can be questioned (Comins and McMurtrie, 1993; Wullschleger et al., 1995). Nevertheless, there is a fundamental connection between physiological and global response, and some constraint on the quantification of the global model parameters from empirical physiological data is desirable. We therefore propose an approximation of the β_i ($i = 1, 2, 3$) in eqs. (16), (20), and (23) as:

$$\beta_i = \mathscr{S}\beta_{E_i}, \tag{24}$$

where β_i is the biotic growth factor for biome NPP, β_E is the experimentally determined β, and $\mathscr{S}$ is a scale translation factor. $\mathscr{S}$ incorporates many assumptions and is itself difficult to quantify precisely; however, it is bounded by $0 \leqslant \mathscr{S} \leqslant 1$.

We estimated β_{E_1} and β_{E_2} from a collection of 164 published photosynthetic CO_2 response curves for 109 C_3 species (Wullschleger, 1993) and the CO_2 response curve published by Collatz et al. (1992) for C_4 plants. The response curves describe the rate of net CO_2 assimilation (A, μ mol CO_2 m^{-2} leaf area s^{-1}) as a function of internal CO_2 partial pressure (c_i, Pa). We converted the internal CO_2 partial pressure of the response curves to internal CO_2 concentration p_i (1 Pa = 10 ppmv) and then to ambient CO_2 concentration p_a using the observations that most C_3 plants have a p_i/p_a ratio χ of 0.7 and C_4 plants a ratio of 0.4. The converted response curves were normalized to $p_a = 350$ ppmv, and the C_3 species were pooled according to the biomes of Table 1. We assumed that tropical grasslands were 100% C_4 and temperate grasslands were 75% C_4. We used nonlinear regression to fit the normalized and pooled response curves with the logarithmic function of eq. (16) (with $p_a^0 = 350$ ppmv) and the modified rectangular hyperbola of eq. (18) (Table 3).

There are no species-specific parameters in the specification of β_3. β_3 does, however, vary with biome as a function of mean biome temperature through the temperature dependency of the photosynthetic CO_2 compensation point Γ^* (eq. (22)) (Table 4). We calculated mean biome temperature (Table 4) as the average temperature for the photosynthetically active season defined by months with mean monthly temperatures greater than −8.4°C (i.e., the temperature at which $\Gamma^* \geqslant 0.0$ and $\beta_3 \geqslant 0.0$). β_3 is derived from a model of C_3 photosynthesis and is probably not appropriate for biomes dominated by C_4 species. We estimated β_3 for these biomes (Tropical and Temperate Grasslands) by first calculating their respective β_3 as if they were pure C_3 biomes. We then reduced these estimates by 50% (Polglase and Wang, 1992).

There are no empirical data to quantify the scaling factor $\mathscr{S}$ of (eq. (24)) for application to long-term biome NPP, and there are little to no data for quantifying its application to ecosystem NPP. Even data at the whole-plant level is limited. Experimental studies of agricultural species have shown that biomass response to elevated CO_2 is

Table 4. *Parameters for the biochemical-based response function of eq. (22)*

Biome	Temperature (°C)	β_{E_3}
tropical moist forest	25.3	0.35
tropical seasonal forest	22.8	0.31
temperate evergreen forest	11.2	0.18
temperate deciduous forest	11.1	0.18
boreal forest	6.5	0.13
tropical woodland and shrubland	26.1	0.36
temperate woodland and shrubland	17.9	0.25
tropical grassland*	26.4	0.18
temperate grassland*	14.2	0.11
tundra and alpine meadow	4.4	0.11
desert scrub	18.2	0.26
cultivated land†	14.0	0.21
pasture land†	14.0	0.21

The parameter β_{E_3} is the biotic growth factor for photosynthesis derived by Polglase and Wang (1992) from the photosynthesis model of Farquhar and von Caemmerer (1982). A function of temperature and CO_2 concentration, β_{E_3} is calculated for the temperatures reported here and an initial atmospheric CO_2 concentration of 276.8 ppmv. The temperatures are area weighted mean temperatures for the photosynthetically active season (see text). Temperature data from a network of climate stations of variable record length (Emanuel et al., 1985) were interpolated to 0.5° latitude and 0.5° longitude resolution and overlain with a map of the model biomes. The biome map is a translation of a 0.5° by 0.5° rendering of the vegetation map of Matthews (1983).

* Half of the β_{E_3} calculated by eq. (22).

† Cultivated and pasture lands are assumed to be converted from temperate ecosystems with a mean annual temperature of 14.0°C.

Table 5. *CO_2 response factors used in the model simulations*

Biome	$\mathscr{S}$	β_1	β_2	β_3
tropical moist forest	0.6	0.32	0.35	0.21
tropical seasonal forest	0.6	0.40	0.32	0.19
temperate evergreen forest	0.6	0.34	0.31	0.11
temperate deciduous forest	0.6	0.43	0.35	0.11
boreal forest	0.6	0.34	0.25	0.08
tropical woodland and shrubland	0.6	0.40	0.29	0.22
temperate woodland and shrubland	0.6	0.35	0.33	0.15
tropical grassland	0.4	0.08	0.002	0.07
temperate grassland	0.45	0.14	0.11	0.05
tundra and alpine meadow	0.6	0.49	0.39	0.07
desert scrub	0.6	0.36	0.27	0.16
cultivated land	0.6	0.34	0.29	0.13
pasture land	0.6	0.40	0.30	0.13

The parameters β_2, β_2 and β_3 are biotic growth factors for NPP response to elevated CO_2. The photosynthetic response factors of Tables 3 and 4 are multiplied by the scaling factor $\mathscr{S}$ to translate from experimental photosynthesis to biome NPP according to eq. (25). Recall that β_2 and β_3 are declining functions of atmospheric CO_2. Values here are for an initial atmospheric CO_2 concentration of 276.8 ppmv.

often less than the response of photosynthetic assimilation (Cure and Acock, 1986; Allen et al., 1987). We used the ratios of biomass accumulation to short-term carbon exchange rate from Cure and Acock (1986) as a rough guide to estimating $\mathscr{S}$ (Table 5). We note that this approximation only crudely accounts for the translation from photosynthesis to NPP and does not incorporate the effect of translation from small-scale controlled exposure studies to a biome-scale response parameter under normal environmental conditions. The true $\mathscr{S}$ is probably smaller than the estimate we use here. The final biome-scale NPP response factors used in the model simulations are shown in Table 5.

3. Results

We initialized the model for 1700 C.E. with an assumed equilibrium global carbon cycle and an atmospheric CO_2 concentration of 276.8 ppmv. We use the standard history of increase in atmospheric CO_2 p_a prescribed by data from the Siple ice core (Friedli et al., 1986) and Mauna Loa Observatory (Keeling et al., 1989) (see Figure 1.3 of Watson et al., 1990). The model's initial conditions and parameter values are in Tables 1–6. Calibration procedures have been described elsewhere (Emanuel et al., 1993; King et al., 1994).

Houghton et al. (1983) provides a comprehensive compilation of the data needed to run our model. Later revisions of these data by Houghton and his colleagues (Houghton et al., 1987) introduce land-use changes that our model does not yet represent (e.g., shifting cultivation in the tropics). Thus, we used the history of land-use change from 1700–1980 given in Appendix 2 of Houghton et al. (1983) to drive our model from it's initial equilibrium. We set rates of harvest $z'_h(t)$ to obtain the annual roundwood production (10^9 kg C yr^{-1}) from Appendix 2 of Houghton et al. (1983) given the estimates of carbon in wood harvested (10^3 kg ha^{-1}) from Table 2 of Houghton et al. (1983). We used the rates of conversion to agriculture from Houghton et al. (1983) to estimate rates of clearing $z'_c(t)$, and we used the negative rates of conversion to agriculture to estimate rates of abandonment $z'_a(t)$. We linearly interpolated the decadal rates of Houghton et al. (1983) to obtain annual rates. Conservatively, we assumed no increase in the rate of land-use change from 1980–1990.

3.1. Simulations

We ran the model with and without CO_2 enhancement of NPP. As expected, CO_2 enhancement of NPP reduces the simulated net carbon flux from the terrestrial biosphere to the atmosphere (Fig. 2). The enhancement of carbon uptake is significant, roughly 0.2–0.5 Gt C yr^{-1} by 1990 with the rectangular-hyperbolic response function yielding the largest effect, but the enhancement is insufficient to bring the model estimates into agreement with the deconvolved estimates of the terrestrial flux (Fig. 3).

Fig. 4 compares our model estimate of land-use CO_2 emissions in the absence of any CO_2 enhancement of NPP with estimates by Houghton et al. (1983) and with more recent estimates from revisions of that analysis. Our estimate uses the Houghton et al. (1983) land-use history, and we used many of the same assumptions, initial conditions, and parameter values. Thus, we obtain similar results. Our use of a dynamic compartment model to describe the fate of carbon in disturbed

Table 6. *Model parameters*

Biome	Inputs			Calibrated†						
	t_m[a]	θ_v[b]	θ_d[c]	ν[d]	ρ[d]	α_{vd}[d]	α_{vs}[d]	α_{ts}[e]	α_{ta}[e]	α_{sa}[f]
tropical moist forest	25.0	0.1	0.1	0.192	0.007	0.041	0.005	0.405	3.645	0.015
tropical seasonal forest	25.0	0.1	0.1	0.189	0.009	0.038	0.004	0.304	2.734	0.011
temperate evergreen forest	25.0	0.1	0.1	0.183	0.009	0.033	0.004	0.038	0.338	0.009
temperate deciduous forest	25.0	0.1	0.1	0.187	0.011	0.036	0.004	0.035	0.312	0.009
boreal forest	25.0	0.1	0.1	0.187	0.016	0.036	0.004	0.012	0.104	0.004
tropical woodland and shrubland	12.0	0.2	0.1	0.393	0.109	0.080	0.020	0.072	0.648	0.011
temperate woodland and shrubland	25.0	0.2	0.1	0.247	0.054	0.080	0.020	0.072	0.648	0.011
tropical grassland	2.5	0.3	0.1	1.640	0.814	0.122	0.052	0.221	1.985	0.028
temperate grassland	5.0	0.3	0.1	1.054	1.047	0.225	0.096	0.079	0.709	0.004
tundra and alpine meadow	5.0	0.3	0.1	0.949	2.442	0.152	0.065	0.009	0.082	0.001
desert scrub	5.0	0.3	0.1	0.839	2.442	0.075	0.032	0.224	2.016	0.002
cultivated land	2.5	0.3	0.1	2.045	2.931	0.406	0.174	0.677	6.090	0.014
pasture land	2.5	0.3	0.1	1.787	2.093	0.225	0.096	0.079	0.709	0.004

† Calibrated for an initial steady state global cycle.
[a] Time to recovery of maximum NPP; half of recovery to maximum carbon density.
[b] Fraction of NPP transferred directly to soil organic matter (Emanuel et al., 1984).
[c] Fraction of litterfall transferred to soil organic matter (Emanuel et al., 1984).
[d] See eq. (8).
[e] See eq. (9).
[f] See eq. (10).

ecosystems instead of the synoptic response functions used by Houghton et al. (1983) has little effect on the estimate of historical CO_2 emissions from land-use change in the absence of CO_2 enhancement of NPP.

Revisions of the 1983 analysis by Houghton and his colleagues have consistently reduced their estimates of CO_2 emissions from land-use change (e.g., Houghton et al., 1987). Current estimates are 1.6 ± 1.0 Gt C yr^{-1} for the decade of 1980–1989 (Houghton et al., 1992) and 0.9 ± 0.4 for 1990 (Dixon et al., 1994), a half to a third of of our

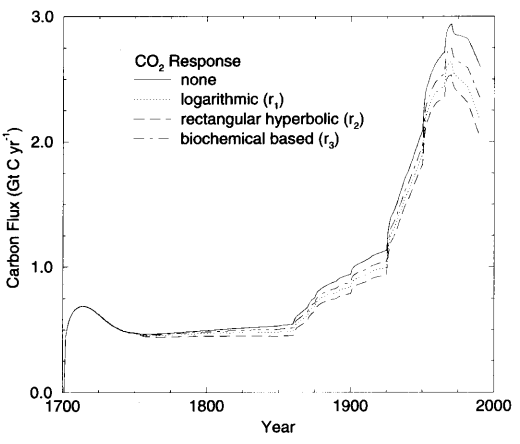

Fig. 2. Simulated global net flux of carbon to the atmosphere from terrestrial ecosystems with and without CO_2 enhancement of NPP.

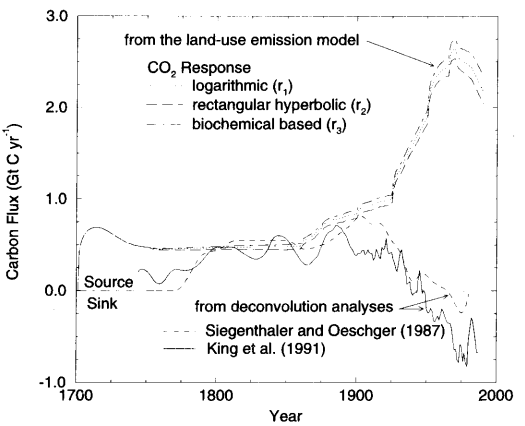

Fig. 3. Estimates of the net exchange of carbon between the atmosphere and terrestrial ecosystems.

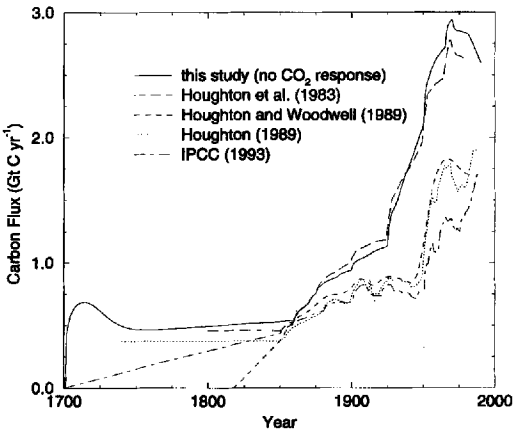

Fig. 4. Simulated global net flux of carbon to the atmosphere from terrestrial ecosystems. The estimates are from models of land-use change and carbon dynamics that do not include CO_2 enhancement of NPP. The curve marked Houghton (1989) is from a paper "The long-term flux of carbon to the atmosphere from changes in land use" presented by R. A. Houghton at the Third International Conference on Analysis and Evaluation of Atmospheric CO_2 Data Present and Past, World Meteorological Organization, Environmental Pollution Monitoring and Research Programme No. 59, Hinterzarten, 1–20 October 1989. The curve is very similar to that of Houghton and Skole (1990).

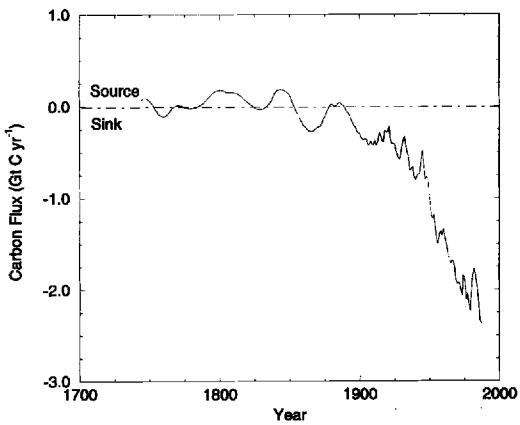

Fig. 5. An estimate of the historical CO_2 enhanced carbon flux (CO_2-ECF) from atmosphere to terrestrial ecosystems. The flux is a hypothesis explaining the historical missing sink.

model's estimate. Thus our model estimates of land-use CO_2 emissions in the absence of a CO_2 response may be too large and may erroneously exaggerate the CO_2 flux that CO_2 enhancement of NPP must compensate.

If we accept recent results from the MBL-TCM (i.e., the IPCC estimate of Fig. 4) as an accurate history of net carbon emissions from changes in land-use and the King et al. (1991) deconvolution with a box-diffusion ocean-atmosphere model (Fig. 3) as an accurate estimate of total net biospheric flux, we can estimate non-land-use biosphere-atmosphere exchange as the difference between these two curves. The difference is an estimate of the missing terrestrial sink. If we ascribe the flux totally to CO_2 enhancement of NPP, we identify the terrestrial sink as a CO_2 enhanced carbon flux (CO_2-ECF) (Fig. 5). Our CO_2-ECF is comparable to the Keeling et al. (1991) biospheric CO_2 fertilization flux (F_{FER}) and the CO_2 enhanced carbon storage (CO_2-ECS) of Polglase and Wang (1992). In our model, it includes the stimulation of CO_2 uptake in ecosystems recovering from land-use disturbance and the stimulation of undisturbed ecosystems. The CO_2-ECF of Fig. 5 is an estimate of the terrestrial sink required for agreement between observed and simulated changes in atmospheric CO_2 (if the IPCC land-use emissions of Fig. 4 are used as input to most contemporary models of the global carbon cycle). The flux history is an expression of the hypothesis that CO_2 enhancement of NPP explains the missing carbon sink. Direct measurements of the flux are not possible, but we can test the hypothesis with model results.

The difference between a modeled flux history with CO_2 enhancement and our model's flux history without CO_2 enhancement is an estimate of CO_2-ECF for a given land-use history. We can also use the model to estimate potential CO_2-ECF in the absence of land-use change. (We run the model without any forcing from land-use change. Specifically, the z_i^t of eqs. (13)–(15) are set to zero for all t. Therefore, all z_i of eq. (12) become zero, and changes in carbon densities and the area distribution of those densities are determined only by time-dependent changes in p_a through eq. (8)). If we assume that changes in terrestrial vegetation caused by land-use change have little or no significant effect on the estimate of CO_2-ECF, we can apply the CO_2-ECF in the absence of land-use change to any independent estimate of land-use

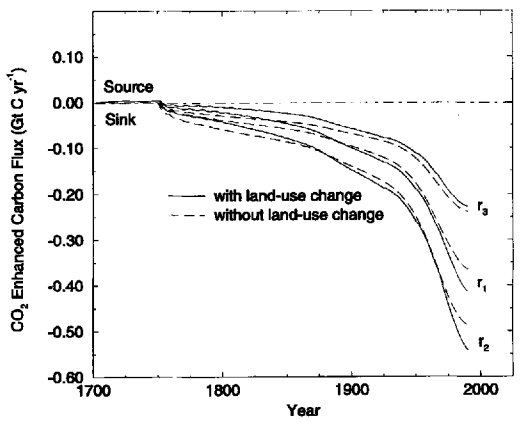

Fig. 6. A comparison of simulated CO_2-ECF made with and without land-use change. The labels r_1, r_1, and r_1 refer to the logarithmic, rectangular-hyperbolic, and biochemical-based CO_2 response functions of eqs. (17), (18), and (25), respectively.

emissions that does not include a CO_2 response, irrespective of the underlying land-use history (e.g., those of Fig. 4). We test that assumption in Fig. 6 by comparing our estimates of CO_2-ECF made with and without land-use change. There is an effect of the perturbed vegetation, but the effect is small, much smaller than the effect of alternative CO_2 response functions. The CO_2 response of large areas of vegetation undisturbed by land use and the CO_2 stimulation of recovery of disturbed areas act together to minimize the difference between CO_2-ECF with and without land-use change. We therefore accept the assumption that land-use change has no significant effect on the global CO_2-ECF, and conclude that we can apply our estimates of CO_2-ECF in the absence of land-use change against the IPCC (1993) estimate of the land-use source to estimate total net biosphere-atmosphere carbon exchange. Accordingly, we can also use our estimates of CO_2-ECF made without land-use change (Fig. 6) to test the hypothesized CO_2-ECF of Fig. 5.

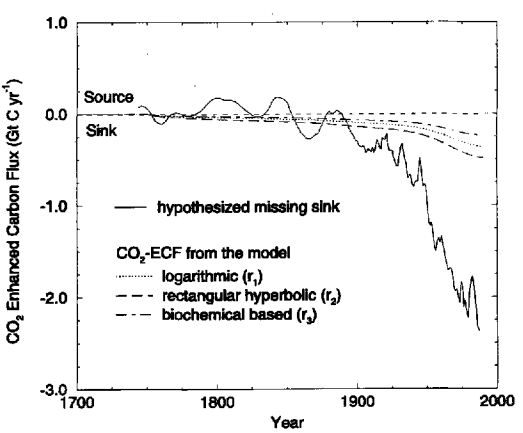

Fig. 7. A comparison of our model estimates of CO_2-ECF with the hypothesized historical missing sink.

Our model estimates of CO_2-ECF are much smaller than the hypothesized historical CO_2-ECF (Fig. 7). By 1990, the difference is as large as 2 Gt C yr^{-1}. The timing of the changes in the modeled CO_2-ECF agrees reasonably with that of the hypothesized sink; both the modeled and hypothesized sinks increase at about 1950, presumably in response to an accelerated increase in atmospheric CO_2. But the intensity of the increase is much less in the modeled CO_2-ECF than in the hypothesized sink. We note that the increase in the sink modeled with the rectangular-hyperbolic response agrees best with the hypothesized sink's increase. The biochemical based response produces the smallest increase. In short, our modeled CO_2-ECF does not match the hypothesized sink.

4. Discussion and conclusion

Our results do not support the hypothesis that CO_2 stimulation of terrestrial carbon uptake and storage explains the missing carbon sink. CO_2-ECF from our model is insufficient to account for the differences between the net biospheric flux estimated by deconvolution and that estimated by modeling land-use change and ecosystem carbon dynamics. CO_2 enhancement of NPP does reduce the estimate of net CO_2 release to the atmosphere, but the enchancement is insufficient to convert the biospheric flux from a net land-use source to a net biospheric sink. Indeed, CO_2 enhancement is insufficient even to reduce the the land-use emissions from an increasing source to a declining source.

These results are independent of the choice of CO_2 response function. The use of the more physiologically-defensible response functions does not substantially alter the results. The most mechanistically based response function, $r_3(p_a)$ from Polglase and Wang (1992), actually yields

1993, Schimel et al., 1994) scales. Temperature enhancement of NPP has been included in several modeling analyses of historical CO_2 records (Esser, 1987; Harvey, 1989; Dai and Fung, 1993; Rotmans and den Elzen, 1993; Vloedbeld and Leemans, 1993; Hudson et al., 1994), and Kohlmaier et al. (1988), Vloedbeld and Leemans (1993), and Hudson et al. (1994) include nitrogen fertilization from anthropogenic nitrogen emissions. Hudson et al. (1994) found a fairly small effect from temperature, while Dai and Fung (1993) concluded that historical variations in temperature and precipitation could account for half of the missing carbon sink. Peterson and Melillo (1985) concluded that nitrogen and phosphorus eutrophication was responsible for a small terrestrial sink in 1980 of about 0.2 Gt C yr^{-1}, a flux comparable to our estimates of CO_2-ECF. On the other hand, Schindler and Bayley (1993) concluded that nitrogen deposition in the past century might be responsible for a 1.0–2.3 Gt C yr^{-1} increase in carbon storage, enough to account for most or all of the missing sink. Hudson et al. (1994) concluded that 40–70% of the fertilization of the terrestrial biosphere may be explained by anthropogenic nitrogen emission. Additional analyses of the contribution of climate change and nitrogen emissions to the missing carbon sink is clearly warranted. However, our model does not yet include these responses, and we limit the remainder of our discussion to the apparently insufficient contribution of terrestrial CO_2 response.

It is of course possible that our estimate of CO_2 enhancement is simply too small. Rotmans and den Elzen (1993) were able to balance the historical carbon budget (matching observed and simulated changes in atmospheric CO_2) by invoking biospheric feedbacks of CO_2 and temperature enhancement of NPP. Their estimate of net biospheric flux closely matches the estimate by deconvolution. Their global β of 0.4 (used in a logarithmic response function) is not much greater than our global average for β_1 of 0.31, and their estimate of land-use emissions without CO_2 enhancement is similar to the IPCC (1993) estimate that we use. They did include an additional temperature response, but the CO_2 effect dominated the temperature effect (Rotmans and den Elzen, 1993). Other models with only CO_2 enhancement have yielded balanced carbon budgets with values of β (i.e., β_1) in the range 0.3–0.5 (Bacastow and Keeling, 1973; Goudriaan and Ketner, 1984; Keeling et al., 1989). Why does our model not balance the carbon budget with comparable, if slightly smaller, values of β?

Is our CO_2-ECF that sensitive to small difference in β? No. When we set the scale translation $\mathscr{S}$ factor in (24) to 1.0 we get comparatively large estimates of β (i.e., those in Tables 3 and 4) and a global mean β_1 of 0.52. With these larger β values, our estimates of CO_2-ECF are still insufficient to explain the missing carbon sink. The estimates of CO_2-ECF for 1990 only increase by approximately 0.25 Gt C yr^{-1}, far short of the increase needed to match our model estimates of CO_2-ECF with our hypothesized CO_2-ECF (see Fig. 7). Even when we set β_1 to an unprecedentedly high 1.0 for all biomes, our model's estimate of CO_2-ECF is insufficient to explain the missing carbon sink. So while our estimates of β could be smaller than the true β, we believe a more likely explanation of our model's comparatively insensitive response to elevated CO_2 lies elsewhere.

We have chosen the logistic function to represent NPP and plant growth (eq. (6)). Our choice is ecologically sound and defensible. Observations of asymptotic biomass accumulations in forests support the choice of a logistic growth curve (Shugart, 1984). However, most global carbon cycle models use different formulations. Bacastow and Keeling (1973) and Keeling et al. (1989), for example, describe NPP as a linear function of vegetation biomass. This assumption is only valid for small changes in atmospheric CO_2 and vegetation biomass, as Keeling and others have pointed out (Keeling, 1973; Bacastow and Keeling, 1973). When ecosystems have been disturbed by land-use change and are recovering from harvest or abandonment from cropland, the linear formulation results in ecologically unrealistic exponential plant growth. Similarly, even a moderate increase in atmospheric CO_2 produces unreasonable exponential plant growth in mature ecosystems. As a consequence, the linear formulation of NPP exaggerates terrestrial carbon storage in response to elevated atmospheric CO_2, and it yields large, and we believe biased, estimates of CO_2-ECF. We believe the representation of NPP as a linear function of biomass is inappropriate in a model of transient land-use disturbance and ecosystem response to historical changes in atmospheric CO_2.

Many other models assume that NPP is independent of plant biomass (Goudriaan and Ketner, 1984; Esser, 1987; Kohlmaier et al., 1987; Polglase and Wang, 1992). The assumption is based on the argument that the canopies of most terrestrial ecosystems are already at or near their maxima. The associated leaf areas exceed that required for complete light interception, and any additional biomass cannot, therefore, increase light interception and thus increase NPP. There is no feedback between biomass and NPP; vegetation response to increased CO_2 is primarily through an increase in quantum yield or photosynthesis per unit leaf area (Kohlmaier et al., 1987; Polglase and Wang, 1992). This assumption is ecologically reasonable for mature ecosystems at or near carbon equilibrium, and, if most terrestrial ecosystems are indeed near equilibrium, the assumption may be valid for global or biome NPP. Interestingly, if we assume this formulation in our model (NPP is independent of vegetation biomass but a function of atmospheric CO_2), our model's estimates of CO_2-ECF (in the absence of land-use change) are closer to the hypothesized historical carbon sink (Fig. 9). The estimates are still too small, however, to explain the missing sink after about 1940 if we assume the standard land use source of IPCC (1993). They do match this later sink if we assume the low estimate of the land-use source (curve L of Fig. 9), but they match the curve poorly prior to about 1950.

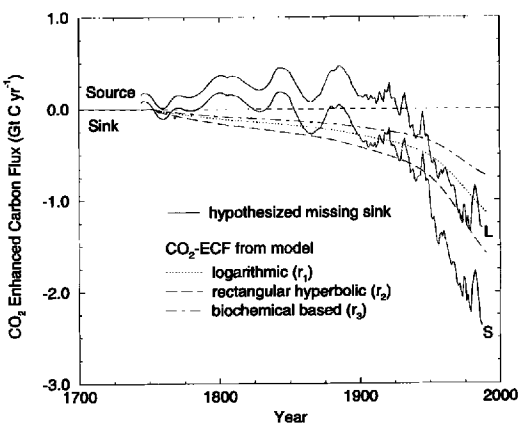

Fig. 9. A comparison of our model estimates of CO_2-ECF with the hypothesized historical missing sink when we assume that NPP is independent of vegetation biomass. Curve S assumes the land-use source history of IPCC (1993); curve L assumes a 63% reduction in the IPCC (1993) history. The β_i of the CO_2 response functions are from Table 5.

The assumption that NPP is independent of biomass is ecologically suspect for ecosystems disturbed by land-use change. It implies that NPP is constant throughout forest recovery and that recovering clearcuts have the same NPP as middle aged and mature forests. The assumption of biomass-independent NPP does generate the desired asymptotic plant grow (i.e., the "concave" biomass curve of Shugart (1984)), but our assumption of logistic plant growth also produces asymptotic plant growth and has patterns of NPP during recovery that more closely match ecological theory and data.

Model assumptions about the relationship between NPP and biomass need greater attention and further consideration. Our model's estimate of CO_2-ECF and its support (or lack of support) for the hypothesis that CO_2 enhancement of NPP explains the missing carbon sink is clearly sensitive to this assumption. We represent NPP as a logistic function of vegetation biomass. Many, if not most, other models use an alternative formulation that favors stronger biosphere response and a larger CO_2-ECF. These models tend to support the hypothesis that CO_2 enhancement of NPP explains the missing carbon sink. Harvey (1989) also assumed that NPP was a logistic function of biomass. Interestingly, Harvey could not balance the historical carbon budget without large values of β, small land-use emissions, and an *additional* miscellaneous sink. We will treat the ecological issues behind the assumptions about NPP and vegetation biomass more fully elsewhere. Given a logistic formulation of NPP, we conclude that our model fails to support the hypothesis that CO_2 enhancement of NPP explains the missing carbon sink. This negative evidence must be weighed against evidence from other models that support the hypothesis.

5. Acknowledgements

The research reported here was sponsored by the Carbon Dioxide Research Program, Environmental Sciences Division, Office of Health and Environmental Research, US Department of Energy, under contract DE-AC05-84OR21400

with Lockheed Martin Energy Systems, Inc., and by the US National Aeronautics and Space Administration Mission to Planet Earth under grant NAWG 2669. This paper is Publication No. 4436, Environmental Sciences Division, Oak Ridge National Laboratory.

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Printed in Belgium