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A first-order analysis of the potential rôle of CO_2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models

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ABSTRACT

We compared the simulated responses of net primary production, heterotrophic respiration, net ecosystem production and carbon storage in natural terrestrial ecosystems to historical (1765 to 1990) and projected (1990 to 2300) changes of atmospheric CO_2 concentration of four terrestrial biosphere models: the Bern model, the Frankfurt Biosphere Model (FBM), the High-Resolution Biosphere Model (HRBM) and the Terrestrial Ecosystem Model (TEM). The results of the model intercomparison suggest that CO_2 fertilization of natural terrestrial vegetation has the potential to account for a large fraction of the so-called "missing carbon sink" of 2.0 Pg C in 1990. Estimates of this potential are reduced when the models incorporate the concept that CO_2 fertilization can be limited by nutrient availability. Although the model estimates differ on the potential size (126 to 461 Pg C) of the future terrestrial sink caused by CO_2 fertilization, the results of the four models suggest that natural terrestrial ecosystems will have a limited capacity to act as a sink of atmospheric CO_2 in the future as a result of physiological constraints and nutrient constraints on NPP. All the spatially explicit models estimate a carbon sink in both tropical and northern temperate regions, but the strength of these sinks varies over time. Differences in the simulated response of terrestrial ecosystems to CO_2 fertilization among the models in this intercomparison study reflect the fact that the models have highlighted different aspects of the effect of CO_2 fertilization on carbon dynamics of natural terrestrial ecosystems including feedback mechanisms. As interactions with nitrogen fertilization, climate change and forest regrowth may play an important role in simulating the response of terrestrial ecosystems to CO_2 fertilization, these factors should be included in future analyses. Improvements in spatially explicit data sets, whole-ecosystem experiments and the availability of net carbon exchange measurements across the globe will also help to improve future evaluations of the role of CO_2 fertilization on terrestrial carbon storage.

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1. Introduction

To help understand the influence of human activities on the global carbon cycle, several studies have developed historical global carbon budgets by quantifying the amount of carbon stored in the atmosphere, oceans and land along with the fluxes among these carbon stocks over time. The budgets are based on our current understanding of the historical rates of: (1) fossil fuel emissions; (2) deforestation and land use change; (3) CO_2 dissolution in oceans; (4) production and decomposition of vegetative tissue. For the most part, sources of carbon to the atmosphere from fossil fuel burning and deforestation are balanced by carbon sinks associated with a number of land and ocean processes including CO_2 dissolution in oceans and plant production. However, a discrepancy or residual has existed between atmospheric sources and land and ocean sinks of carbon over time. This discrepancy was between 0.5 to 2.6 Pg C yr^{-1} during the 1980s and early 1990s (Melillo et al., 1996b). Several lines of evidence, including measurements of the oxygen/nitrogen ratio of the atmosphere since 1990 (Keeling et al., 1996), indicate that the discrepancy, often referred to as the "missing carbon sink," is due to the underestimation of CO_2 uptake by terrestrial vegetation.

Several mechanisms have been proposed to account for a higher uptake of carbon by vegetation. These include: (1) enhanced plant productivity due to the stimulation of photosynthesis by higher atmospheric concentrations of CO_2, i.e. "CO_2 fertilization" (Friedlingstein et al., 1995); (2) enhanced plant productivity due to the anthropogenic deposition of nitrogen on vegetation near industrialized regions, i.e., "N fertilization" (Melillo and Gosz, 1983; Peterson and Melillo, 1985; Hudson et al., 1994; Townsend et al., 1996; Holland et al., 1997); (3) the effects of climate variations on plant production and decomposition (Dai and Fung, 1993; Braswell et al., 1997); and (4) regrowth of forests (Houghton et al., 1987; Melillo et al., 1988, 1996a; Harmon et al., 1990; Dixon et al., 1994). To explore the potential of the CO_2 fertilization mechanism in more detail, we conducted a modeling experiment using terrestrial biosphere models as part of the Carbon Cycle Model Linkage Project (CCMLP) sponsored by the Electrical Power Research Institute.

Since 1958, increases in the atmospheric concentration of carbon dioxide have been well documented (Keeling et al., 1995). These increases are expected to continue in the future as a result of human activities, especially fossil fuel combustion (IPCC, 1995). Experimental studies have shown that increased CO_2 concentrations can lead to increased plant growth (Kimball, 1975; Gates, 1985; Bazzaz, 1990; Idso and Idso, 1994; McGuire et al., 1995). However, it is less clear whether elevated CO_2 concentrations also result in increased carbon storage at an ecosystem level. Some field studies and studies in artificial ecosystems show small or statistically insignificant responses to elevated CO_2 concentrations (D'Arrigo and Jacoby, 1993; Körner and Arnone III, 1992; Oechel et al., 1993; Owensby et al., 1993, 1996; Hungate et al., 1997b). Terrestrial biosphere model simulations of equilibrium climate change scenarios associated with doubled CO_2 (Melillo et al., 1993; Xiao et al., 1997; McGuire et al., 1997) have suggested that enhanced CO_2 concentrations may contribute to the response of global vegetation to future climate change. Model simulations with historical atmospheric CO_2 concentrations (Friedlingstein et al., 1995; Post et al., 1997) have suggested that CO_2 fertilization may have accounted for about 69 to 75% of the "missing carbon" described above. On the other hand, the modeling study of King et al. (1995) suggests that CO_2 fertilization can only explain about 20% of the terrestrial sink required to balance the global carbon budget. Bruno and Joos (1997) also suggest that the temporal evolution of the biospheric sink cannot be explained by CO_2 fertilization alone based on a deconvolution analysis that separates the magnitudes of the atmospheric, oceanic and terrestrial sinks through time.

Because our knowledge of ecosystem processes is imperfect, different models emphasize different relationships to describe these processes. These differences contribute to the uncertainty in estimates of primary production and carbon storage of the terrestrial biosphere and the uncertainty of how terrestrial carbon dynamics will respond to changes in atmospheric CO_2 concentration or climate (VEMAP Members, 1995). To examine how differences in basic model assumptions may affect predicted responses of the terrestrial biosphere to increasing atmospheric CO_2 concentrations, we use four terrestrial biosphere models: the

Bern model (Bern); the Frankfurt Biosphere Model (FBM); the High-Resolution Biosphere Model (HRBM); and the Terrestrial Ecosystem Model (TEM).

2. Methods and materials

2.1. Overview

To explore the potential influences of CO$_2$ fertilization on carbon dynamics in terrestrial ecosystems, we examine the responses of net primary production, heterotrophic respiration, net ecosystem production, vegetation carbon, soil carbon and total carbon storage, as estimated by the four terrestrial biosphere models, to historical and projected future changes in atmospheric CO$_2$ concentration. The Bern model, which has been used by IPCC for CO$_2$ scenario calculations (Schimel et al., 1996), simulates carbon dynamics of the whole terrestrial biosphere without geographic specificity whereas FBM, HRBM and TEM develop spatially explicit estimates of carbon fluxes and pools across the globe. We first compare the global results of these spatially explicit models to the results of the terrestrial component of the Bern model at the beginning of the study period to examine differences in initial carbon fluxes and stocks assumed by the models. We then compare the response of the terrestrial biosphere to historical changes in atmospheric CO$_2$ concentration and to future changes in atmospheric CO$_2$ concentration (Fig. 1) described by the S650 stabilization profile of the Intergovernmental Panel on Climate Change (Enting et al., 1994). Finally, we examine how model assumptions influence the projected response of the terrestrial biosphere to CO$_2$ fertilization.

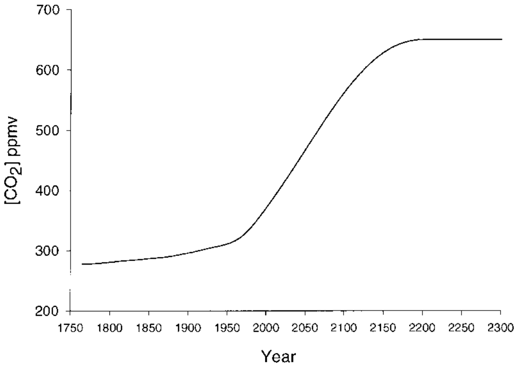

Fig. 1. Atmospheric CO$_2$ concentration from 1765 to 2300 as prescribed by the IPCC S650 concentration profile.

2.2. Model descriptions

Although all of these models simulate the exchange of carbon between the atmosphere and the terrestrial biosphere, they use different approaches (Table 1) for estimating the uptake of atmospheric CO$_2$ by vegetation as represented by net primary production (NPP). The Bern model assumes that a baseline NPP rate (NPP$_0$) is modified only by changes in atmospheric CO$_2$ concentrations using a β factor approach described later. The HRBM uses statistical relations of NPP with temperature and precipitation which are then modified as a function of atmospheric CO$_2$ concentrations and soil characteristics. In FBM and TEM, NPP is estimated as the difference of gross primary production (GPP) and plant respiration (R_A). The effects of environmental factors, including changing atmospheric CO$_2$ concentrations, on GPP and R_A are calculated with a multiplicative approach in these models.

In addition to plant respiration, terrestrial carbon is returned to the atmosphere by the decomposition of organic matter and respiration of consumers (e.g., animals), known collectively as heterotrophic respiration (R_H). The flux R_H is calculated in all the spatially explicit models by relationships that depend on soil carbon, temperature, and soil moisture, but the formulations of the relationships or the parameters of similar formulations may differ among the models (Heimann et al., 1998). In the Bern model, R_H is calculated using constant rate coefficients that do not depend on climate.

The difference between NPP and R_H represents the net storage of carbon in the terrestrial biosphere and is known as net ecosystem production (NEP). Net ecosystem production will be positive when the terrestrial biosphere is a sink for atmospheric CO$_2$ and negative when the terrestrial biosphere is a source of atmospheric carbon. Thus, carbon storage increases when either plant production is enhanced or decomposition is inhibited. Conversely, less carbon is stored in terrestrial

Table 1. *Comparison of how the terrestrial biosphere models estimate net primary productivity (NPP) and heterotrophic respiration* (R_H)

Model[a]	Temporal resolution of NPP	NPP calculated as:	Influenced by[b]:	No. of VEGC pools	No. of SOILC[c] pools	Reference
Bern	annual	NPP	$\mathrm{NPP} = \mathrm{NPP}_0\, f(\mathrm{CO_2})$	2	2	Siegenthaler and Oeschger (1987); Joos et al. (1996)
HRBM 3.0	monthly	NPP	$\mathrm{NPP} = f(\mathrm{CO_2}, \mathrm{FERT})\, f(\mathrm{T}, \mathrm{PPT})\, f(\mathrm{AET})$ $R_H = \mathrm{SOILC}\, f(\mathrm{T})\, f(\mathrm{PPT})$	4	5	Esser et al. (1994)
FBM 2.2	daily	$\mathrm{GPP} - R_A$	$\mathrm{GPP} = f(\mathrm{CO_2}, \mathrm{T})\, f(\mathrm{PAR}, \mathrm{LAI})\, f(\mathrm{T})\, f(\mathrm{SW})$ $R_A = \mathrm{VEGC}\, f(\mathrm{T})$ $R_H = \mathrm{SOILC}\, f(\mathrm{T})\, f(\mathrm{SW})$	2	1	Kindermann et al. (1993); Lüdeke et al. (1994); Kohlmaier et al. (1997)
TEM 4.1	monthly	$\mathrm{GPP} - R_A$	$\mathrm{GPP} = \mathrm{f}(\mathrm{CO_2}, \mathrm{AET/PET})\, f(\mathrm{PAR})\, f(\mathrm{T})\, f(\mathrm{N})$ $\mathrm{R_A} = (\mathrm{VEGC}\, f(\mathrm{T})) + f(\mathrm{GPP})$ $\mathrm{R_H} = \mathrm{SOILC}\, f(\mathrm{T})\, f(\mathrm{SW})$	1	1	Tian et al. (this issue); Xiao et al. (1998)

[a] FBM is the Frankfurt Biosphere Model; HRBM is the High-Resolution Biosphere Model; and TEM is the Terrestrial Ecosystem Model.

[b] $\mathrm{NPP_0}$ is a baseline NPP ($60\ \mathrm{Pg\ C\ yr^{-1}}$) used in the Bern model; GPP is gross primary productivity; R_A is autotrophic respiration; VEGC is vegetation carbon (i.e., carbon in leaves, sapwood, heartwood, roots, etc.); PAR is photosynthetically active radiation at the top of the canopy; LAI is leaf area index; T is air or soil temperature; PPT is precipitation; AET is actual evapotranspiration; PET is potential evapotranspiration; SW is soil water; $\mathrm{CO_2}$ is atmospheric carbon dioxide concentration; FERT is soil fertility factor; N is nitrogen.

[c] SOILC includes litter from herbaceous and woody phytomass, and soil organic carbon.

ecosystems if plant production is inhibited or decomposition is enhanced.

All the spatially explicit models in this study consider carbon and water dynamics, but TEM also includes nitrogen dynamics. These models, however, use different temporal scales to estimate NPP and R_H. In HRBM and TEM, climate data enter into the flux calculations as monthly means while FBM uses a daily time step. Additional information on the calculation of NPP and R_H by the models used in this study can be found in the references provided in Table 1. In all the models, atmospheric CO_2 concentration influences GPP or NPP, but this influence is moderated by additional environmental factors in the spatially explicit models (Table 1). Interestingly, the spatially explicit models use different environmental factors to moderate the direct influence of atmospheric CO_2 on primary production: FBM uses air temperature; HRBM uses soil fertility; and TEM uses actual and potential evapotranspiration. In these models, heterotrophic respiration is not directly influenced by changes in atmospheric CO_2, but changes in NPP and litterfall affect the amount and composition (e.g., woody, herbaceous) of litter and soil organic matter available for decomposition so R_H is indirectly influenced by changes in atmospheric CO_2.

Below, we take a closer look at how the models simulate the influence of atmospheric CO_2 concentration on NPP or GPP. The algorithms used by FBM, HRBM and TEM to calculate NPP and R_H have been compared in an earlier study (Heimann et al., 1998).

Bern model (Bern). Enhancement of plant growth due to elevated CO_2 concentration is described in the Bern model as a logarithmic function of the changes in atmospheric CO_2:

$$f(CO_2) = 1 + \beta_{LOG}[\ln(CO_2/CO_{20})] \qquad (1)$$

where CO_{20} is the pre-industrial atmospheric CO_2 level. A value of 0.287 was selected for the beta factor (β_{LOG}) in order to balance the global carbon budget while assuming an average land use emission of 1.1 Pg C yr^{-1} during the 1980–89 decade.

High-Resolution Biosphere Model (HRBM). The model assumes that enhanced atmospheric CO_2 concentrations increase NPP more on productive soils than on less productive soils. The influence of atmospheric CO_2 on NPP is modified by soil fertility (FERT) in HRBM:

$$f(CO_2, \text{FERT}) = A[1.0 - \exp^{\{\ln(1.0-1/A)(\text{Ca}-80)/240\}}], \qquad (2)$$

$$A = 1.0 + [F(\text{m})/4.0], \qquad (3)$$

where F(m) is a factor that characterizes the fertility of the main FAO soil units of the world and ranges from 0.03 to 2.78 (Esser et al., 1994, Esser, 1995); Ca is atmospheric CO_2 concentration (ppmv). An atmospheric CO_2 concentration of 80 ppmv is assumed to be the compensation point between gross photosynthesis and photorespiration on the uptake of atmospheric CO_2. The parameters, 4.0 and 240, are empirically derived from relationships of NPP to atmospheric CO_2 concentration and have no physiological meaning. Equation (2) is used to correct NPP for the actual atmospheric CO_2 concentration.

Frankfurt Biosphere Model (FBM). The influence of atmospheric CO_2 on GPP is modified by air temperature in FBM to account for the temperature dependence of the compensation point between gross photosynthesis and photorespiration on the uptake of atmospheric CO_2:

$$f(CO_2, T) = [\text{Ci} - \Gamma^*(T)]/[\text{Ci} + 2\Gamma^*(T)], \qquad (4)$$

where the internal CO_2 concentration (ppmv) of leaves (Ci) is assumed to be 70% of the atmospheric CO_2 concentration (Wong et al., 1979) and the CO_2 compensation point for gross photosynthesis and photorespiration, $\Gamma^*(T)$, at any temperature (°C) is given by Kirschbaum (1993):

$$\Gamma^*(T) = 40.6\, e^{\{9.46(T-25)/(T+273.2)\}}. \qquad (5)$$

The response of the maximum assimilation rate, α, to increased CO_2 concentration can then be described (Kirschbaum and Farquhar, 1987; McMurtrie, 1993) with:

$$\alpha(CO_2, T) = \alpha(CO_2, T)_{350} \times [f(CO_2, T)/f(CO_2, T)_{350}], \qquad (6)$$

where $\alpha(CO_2, T)_{350}$ is the maximum assimilation rate under current temperatures and atmospheric CO_2 concentration (350 ppmv).

Terrestrial Ecosystem Model (TEM). The influence of atmospheric CO_2 on GPP is modified by evapotranspiration in TEM to account for the effect of stomatal conductance of atmospheric CO_2

into leaves:

$$f(\mathrm{CO_2}, \mathrm{AET/PET}) = C_i/(k_c + C_i) \tag{7}$$

$$C_i = C_a G_V \tag{8}$$

for AET/PET $\leqslant 0.1$

$$G_V = -10.0(\mathrm{AET/PET})^2 + 2.9(\mathrm{AET/PET}) \tag{9a}$$

for AET/PET > 0.1

$$G_V = 0.1 + 0.9(\mathrm{AET/PET}) \tag{9b}$$

where k_c is the half saturation constant (400 ppmv); C_i is the intracellular concentration of CO_2 in the canopy (ppmv); C_a is atmospheric CO_2 concentration; G_V is relative canopy conductance; AET is actual evapotranspiration (mm); and PET is potential evapotranspiration (mm). The half saturation constant k_c has been chosen to increase $f(\mathrm{CO_2}, \mathrm{AET/PET})$ by 37% for a doubling of atmospheric CO_2 from 340 ppmv to 680 ppmv when G_V equals 1.0. Increases in leaf area are assumed in TEM to compensate for decreases in transpiration per unit leaf area (Eamus and Jarvis, 1989) so that overall canopy conductance and AET do not change in response to elevated CO_2 concentrations (Pan et al., 1998).

In previous studies (Melillo et al., 1993; McGuire et al., 1993, 1997; VEMAP Members, 1995; Pan et al., 1998), the response of NPP to elevated CO_2 has also been shown to be constrained by nitrogen availability in TEM simulations. Because rates of nitrogen mineralization are generally higher in warmer climates, this nitrogen constraint has been most restrictive in temperate and boreal ecosystems.

2.3. *Model input data*

In this study, climate does not change from year to year. The fixed climate is taken from an updated version of the Leemans and Cramer (1991) database, which provides spatially explicit inputs of temperature, precipitation and solar radiation. These gridded data are long-term (1931–1960) monthly mean values with the entire land surface (except Antarctica) represented by 62,483 grid cells. Each grid cell has a spatial resolution of 0.5° latitude × 0.5° longitude. If necessary, the monthly values were interpolated to daily and hourly timesteps using simple interpolation schemes and periodic functions. The long-term climate data set has been used to represent climate conditions for each year from 1765 to 2300. Although each spatially explicit model uses the same atmospheric CO_2 data and climate data in this study, the models use different vegetation and soils data sets to estimate carbon fluxes and pools of the terrestrial biosphere. All the spatially explicit models use data sets representing potential vegetation, i.e., no human disturbance, but the distribution and classification of vegetation varies among these data sets: FBM uses a map derived from Matthews (1983); TEM uses a map described in Melillo et al. (1993); and HRBM uses the vegetation distribution results of the BIOME model (Prentice et al., 1992). The descriptions of soil characteristics, such as soil type and texture, are different among the models, but all soils data are based on the FAO soil map of the world (FAO/UNESCO, 1974).

2.4. *Simulation protocol*

Before running the models with the historical and future atmospheric CO_2 data, each of the spatially explicit models (HRBM, FBM, TEM) simulated equilibrium terrestrial carbon dynamics for each grid cell using the gridded data sets described above and an atmospheric CO_2 concentration of 278 ppmv. The models assume equilibrium conditions are reached when annual NEP is equal to zero, i.e., annual NPP is equal to annual R_H. For TEM, the annual fluxes of net nitrogen mineralization, litterfall nitrogen, and nitrogen uptake by vegetation must also be balanced and nitrogen inputs to the ecosystem must equal nitrogen losses at equilibrium.

The four terrestrial biosphere models then use the same historical and future atmospheric CO_2 data to calculate terrestrial carbon fluxes and pools from 1765 to 2300. The spatially explicit models also use the same gridded climate data sets described above for the transient simulations. Because we assume that CO_2 fertilization will affect carbon storage only in areas that have been minimally affected by human activities (i.e., natural areas) in this first order analysis, we consider changes in carbon fluxes and stocks estimated by the spatially explicit models only in these natural areas (Fig. 2). We also assume that land use has remained constant over the study period. Thus, our analysis does not consider the effects of land use change on historical carbon stocks and fluxes from terrestrial ecosystems. Natural areas have

Fig. 2. Distribution of natural ecosystems used by the Terrestrial Ecosystem Model. The Frankfurt Biosphere Model used the vegetation map of Matthews (1983) and the High-Resolution Biosphere Model used the potential vegetation distribution of Prentice et al. (1992) to represent the distribution of natural vegetation. Cultivated lands (grey) were excluded from analyses of the estimates by all the spatially explicit models.

been delimited based on the descriptions of contemporary vegetation by Olson (1992). Thus, the estimates of carbon fluxes and stocks of the spatially explicit models are based on 52 461 grid cells. In the Bern model, the results presented here also do not include changes in carbon stocks and fluxes induced by land use change to allow a consistent comparison with the results of the spatially explicit models. However, carbon stocks and fluxes from cultivated lands are included in the Bern model estimates because the model simulates carbon dynamics of the whole terrestrial biosphere without geographic specificity.

2.5. *Examination of terrestrial sink dynamics*

As described by Thompson et al. (1996), the size of a stable terrestrial sink after a long period of increase in NPP can be described in terms of the initial NPP, the relative rate of increase in NPP and the turnover time of carbon in the system. To examine the relative importance of these factors on the terrestrial sinks estimated by the terrestrial models in this study, we calculate "effective" β factors from NPP estimates of the models and mean residence times of carbon from model estimates of vegetation carbon, soil carbon, NPP and heterotrophic respiration.

Calculation of "effective" β factors. The influence of CO$_2$ fertilization on NPP is often described and compared among models with the use of a β factor in which relative changes in NPP over time are compared to relative changes in atmospheric CO$_2$ concentration. We calculated "effective" β factors, based on the formulation assumed in the Bern model, from the NPP estimates of the four terrestrial models and the corresponding atmospheric CO$_2$ concentrations used as model input in this study as diagnostic variables to compare the NPP responses to CO$_2$ fertilization among the terrestrial biosphere models. The Bern model assumes that the β factor (β_{LOG}) describes a logarithmic dependency between additional net primary productivity and atmospheric CO$_2$ (Bacastow and Keeling, 1973; Enting et al., 1994):

$$\beta_{\mathrm{LOG}} = \frac{(\mathrm{NPP}_t - \mathrm{NPP}_0)/\mathrm{NPP}_0}{\ln(\mathrm{CO}_{2t}/\mathrm{CO}_{20})}, \tag{10}$$

where NPP_t and CO_{2t} are the NPP and atmospheric CO_2 concentration at time t; and NPP_0 and CO_{20} are the initial NPP and atmospheric CO_2 concentration, respectively. For this study, we assume that CO_{20} is 278 ppmv.

To examine potential effects of the stabilization of atmospheric CO_2 on the response of NPP to CO_2 fertilization, we calculate "effective" β factors of four time periods: (1) 1765 to 1990; (2) 1765 to 2050; (3) 1765 to 2200; (4) 1765 to 2300.

Calculation of mean residence times (τ). Because we do not assume that equilibrium conditions exist under our transient simulations, we cannot calculate the turnover times of carbon in the terrestrial biosphere. However, we calculate the mean residence times of carbon in various compartments of the terrestrial biosphere as diagnostic variables to examine differences in the dynamics of carbon storage among the terrestrial biosphere models. The mean residence time of the terrestrial biosphere (τ_{TOTAL}) is calculated as:

$$\tau_{\mathrm{TOTAL}} = (\mathrm{VEGC}_t + \mathrm{SOILC}_t)/R_{\mathrm{H}_t}, \qquad (11)$$

where VEGC_t is the sum of all standing vegetation components during year t; SOILC_t is the sum of all standing litter and soil organic matter components during year t; and R_{H_t} is the annual flux of heterotrophic respiration during year t. Because we are particularly interested in the residence time of the carbon added to the biosphere as a result of CO_2 fertilization, we calculate the mean residence time of this excess carbon (τ_{ex}) as:

$$\tau_{\mathrm{ex}} = [(\mathrm{VEGC}_t + \mathrm{SOILC}_t) - (\mathrm{VEGC}_0 + \mathrm{SOILC}_0)]/(R_{\mathrm{H}_t} - R_{\mathrm{H}_0}), \qquad (12)$$

where VEGC_0 represents the initial standing stock of vegetation carbon in 1765; SOILC_0 represents the initial standing stock of soil organic carbon and litter carbon in 1765; and R_{H_0} is the annual flux of heterotrophic respiration in 1765. If a model has a refractive carbon pool that hardly contributes to the exchange of carbon with the atmosphere (e.g., woody tissue, passive soil organic matter), it would be reflected in τ_{TOTAL}, but not in τ_{ex}.

To examine model differences in how this carbon is stored in the terrestrial biosphere, we calculate the mean residence time for the excess carbon in vegetation and soils. Because TEM represents vegetation as a single carbon pool, we determine the mean residence time of vegetation (τ_{VEG}) for all models as follows:

$$\tau_{\mathrm{VEG}} = (\mathrm{VEGC}_t - \mathrm{VEGC}_0)/(\mathrm{LTRFALL}_t - \mathrm{LTRFALL}_0) \qquad (13)$$

where $\mathrm{LTRFALL}_t$ is the annual carbon flux from vegetation to soil and litter pools during year t and is calculated as follows:

$$\mathrm{LTRFALL}_t = \mathrm{NPP}_t - (\mathrm{VEGC}_t - \mathrm{VEGC}_{t-1}). \qquad (14)$$

$\mathrm{LTRFALL}_0$ is assumed to equal NPP in 1765. Because TEM also represents litter and soil organic matter as one carbon pool, we determine the mean residence time of the excess carbon in soils (τ_{SOIL}) as follows:

$$\tau_{\mathrm{SOIL}} = (\mathrm{SOILC}_t - \mathrm{SOILC}_0)/(R_{\mathrm{H}_t} - R_{\mathrm{H}_0}). \qquad (15)$$

To examine how stabilization of atmospheric CO_2 may effect estimates of the mean residence times, we calculate the turnover times described above for four time periods: (1) 1765 to 1990; (2) 1765 to 2050; (3) 1765 to 2200; (4) 1765 to 2300.

3. Results

At the beginning of the study period, the spatially explicit models develop similar estimates of NPP and R_{H} (30.9 to 33.2 Pg C yr^{-1}; see Table 2) for all the designated natural areas across the globe. Because these natural areas are assumed to be covered with undisturbed, climax vegetation before 1765, no net storage of atmospheric carbon (i.e., $\mathrm{NEP} = 0$) is estimated to occur in any of these ecosystems during 1765.

Initial estimates of carbon storage in these natural areas (Table 2), however, do vary among the spatially explicit models. Total carbon storage ranges from 1029 Pg C in FBM to 1923 Pg C in HRBM. Both FBM and TEM estimate that about half of this carbon is stored in soils whereas HRBM estimates that 70% of this carbon is stored in soils. Estimates of soil organic carbon by TEM do not include soil organic matter which is assumed to be biologically unreactive in the context of global change that might occur in the next century or so. In previous studies with TEM, the biologically unreactive soil carbon has been estimated to represent 400 to 500 Pg C of the global soil carbon inventory (Melillo et al., 1995; McGuire et al., 1997). With the inclusion of the

Table 2. *Comparison of carbon fluxes (Pg C yr^{-1}) and stocks (Pg C) among the four terrestrial biosphere models for the years 1765 to 2300*

Variable	Bern	HRBM	FBM	TEM
Net primary productivity				
1765	60.0	30.9	33.2	31.3
1860	60.6	31.6	34.4	32.2
1980	63.4	34.3	38.3	33.9
1990	64.2	35.0	39.4	34.2
2050	68.9	38.2	44.5	35.2
2200	74.6	40.1	48.6	35.3
2300	74.6	40.1	48.6	35.3
Heterotrophic respiration				
1765	60.0	30.9	33.2	31.3
1860	60.4	31.4	34.0	31.9
1980	62.4	33.2	36.5	33.3
1990	62.9	33.7	37.2	33.5
2050	66.8	36.4	41.8	34.4
2200	73.6	39.3	47.9	35.2
2300	74.3	39.7	48.3	35.3
Net ecosystem productivity				
1765	0.0	0.0	0.0	0.0
1860	+0.2	+0.2	+0.4	+0.3
1980	+1.0	+1.1	+1.8	+0.6
1990	+1.3	+1.3	+2.2	+0.7
2050	+2.1	+1.8	+2.7	+0.8
2200	+1.0	+0.8	+0.8	+0.1
2300	+0.3	+0.4	+0.3	0.0
Total carbon storage				
1765	2220	1923	1029	1146
1860	2230	1935	1049	1162
1980	2278	1994	1130	1211
1990	2289	2006	1150	1220
2050	2393	2107	1306	1267
2200	2663	2309	1584	1346
2300	2725	2364	1631	1346
Vegetation carbon				
1765	600	577	490	575
1860	605	584	505	587
1980	626	613	560	616
1990	631	620	575	619
2050	675	669	683	635
2200	745	733	812	640
2300	746	738	813	637
Soil carbon				
1765	1620	1346	538	570
1860	1625	1351	544	575
1980	1653	1381	570	596
1990	1658	1386	574	600
2050	1717	1438	623	632
2200	1918	1576	772	706
2300	1979	1626	818	709

biologically unreactive soil carbon, TEM estimates of soil carbon and total carbon storage are still less than the comparable estimates by HRBM, but a larger proportion (63 to 65%) of the estimated terrestrial carbon would be assumed to be stored in soils.

The Bern model assumes terrestrial NPP and R_H in 1765 (60.0 Pg C yr^{-1}) to be almost twice the comparable estimates of the spatially explicit models (Table 2). Total carbon storage assumed by the Bern model in 1765 (2220 Pg C) is about twice the comparable estimates of FBM and TEM. About 73% of this carbon is assumed to be stored in soils. Unlike the spatially explicit models, the Bern estimates also include carbon fluxes and storage in areas historically disturbed by human activities.

3.1. *Response of the terrestrial biosphere to historical changes in atmospheric CO$_2$ concentration*

In all models, estimates of both annual NPP and annual R_H increase over time in response to historical increases in atmospheric CO$_2$ concentration, but the increases in annual R_H lag the comparable increases in NPP so that NEP also increases over time (Fig. 3). From 1765 to 1990, the models estimate that annual NPP increases by 2.9 to 6.2 Pg C yr^{-1} and that annual R_H increases by 2.2 to 4.0 Pg C yr^{-1} (Table 2). The FBM estimates the largest absolute and relative increases in NPP (+18.7%) and R_H (+12.0%) whereas the TEM estimates the smallest absolute increases in NPP and R_H and the Bern model estimates the smallest relative increases in NPP (+7.0%) and R_H (+4.8%).

The lag between NPP and R_H causes NEP to increase by 0.7 to 2.2 Pg C yr^{-1} in 1990. Again, the largest increase in NEP is estimated by FBM and the smallest increase in NEP is estimated by TEM. The Bern model and HRBM estimate the same increase in NEP. The NEP estimates of all the models from 1980 to 1990 (Table 2) are roughly in accordance with the recent IPCC budget for the decade of the 1980s (Schimel et al., 1996) that estimates a terrestrial sink due to ecosystem physiological processes of 1.3 ± 1.5 Pg C yr^{-1}, and with historical estimates of the "missing carbon sink" (Fig. 3b) as determined from deconvolution analyses (Bruno and Joos, 1997).

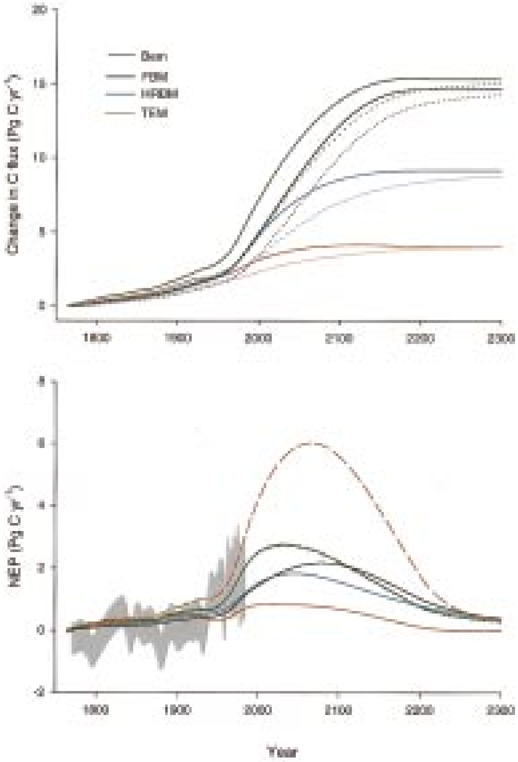

Fig. 3. Changes in (a) global net primary productivity (solid lines) and heterotrophic respiration (dotted lines); and (b) global net ecosystem productivity (NEP) estimated by the four terrestrial biosphere models (Bern, FBM, HRBM, TEM) and the "carbon only" version of TEM between 1765 and 2300 in response to changes in atmospheric CO_2 concentration represented by the IPCC S650 profile. The shaded area represents the 1–σ uncertainty band associated with the terrestrial carbon sink required to balance the global carbon budget as determined from deconvolution analyses (Bruno and Joos, 1997). The dashed red line in (b) represents NEP estimates from a "carbon only" parameterization of the terrestrial ecosystem model such that carbon uptake by vegetation is not limited by nitrogen availability.

However, none of the models are able to depict the rapid and large change (0.8 Pg C yr^{-1}) in carbon storage between 1933 and 1943 as obtained by the deconvolution analysis. Instead, the spatially explicit models estimate a "dip" in NEP around the 1950s (Fig. 3b).

A decline in the growth rate of atmospheric CO_2 concentration during the 1930s and 1940s, caused by the slower increase in fossil fuel emissions during this period, causes a decline in the simulated growth rates of NPP over this period. At first, simulated R_H continues to increase unabated during this period so that the difference between NPP and R_H decreased, but then the growth rates of R_H also began to decline until the 1950s when atmospheric CO_2 concentrations again began to increase more rapidly.

The low NEP estimate by TEM is a result of carbon uptake being tightly constrained by nitrogen availability in TEM. No additional nitrogen inputs (i.e., the N-fertilization effect) are considered in this experiment.

The NEP results from the spatially explicit models suggest that the effect of CO_2 fertilization on terrestrial ecosystems is not uniform over the surface of the earth. In 1990, all of these models estimate a bimodal distribution of terrestrial sinks (i.e., positive NEP) across latitudes with a large tropical sink between 15°S and the equator and another smaller temperate/boreal sink between 45° to 60°N (Table 3). However, most of this annual carbon gain in tropical regions estimated by HRBM and FBM occurs in tropical rain forests (Fig. 4). In contrast, most of the annual carbon gain in tropical regions estimated by TEM in 1990 occurs in drier areas, such as the cerrado in Brazil or tropical savannas in Africa. The models also vary in the estimated size of these terrestrial sinks in 1990. The HRBM and FBM estimates of tropical NEP are between three to five times larger than the corresponding TEM estimates in the 15° to 0°S latitudinal band and between two to four times larger in the 45° to 60°N latitudinal band.

The simulated increases in NEP over the historical time period suggest that a substantial amount of carbon released to the atmosphere through human actions could have been stored in terrestrial ecosystems as a result of CO_2 fertilization. From 1765 to 1990, the simulated amount of carbon stored in natural areas is estimated to have increased by 74 to 121 Pg C by the spatially explicit models (Table 2). The FBM again estimates the largest increase whereas the TEM estimates the smallest increase in terrestrial carbon storage. The TEM estimate is closest to the 69 Pg C increase in carbon storage estimated by the Bern model, although the Bern model does consider both natural areas and areas disturbed by human activities.

With the exception of TEM, the latitudinal distribution of the historical (1765 to 1990)

Table 3. *Comparison of the latitudinal distribution of net ecosystem productivity (NEP) in 1990 (Pg C yr^{-1}) and changes in vegetation carbon, soil carbon and total carbon (Pg C) among the three spatially explicit models (HRBM, FBM, TEM)*

Latitudinal band	Model	NEP in 1990	1765 to 1990			1990 to 2300		
			Veg. C	Soil C	Total C	Veg. C	Soil C	Total C
75 to 90°N	HRBM	0.00	0.01	0.02	0.03	0.00	0.15	0.15
	FBM	0.00	0.08	0.01	0.09	−0.08	0.04	−0.04
	TEM	0.00	0.01	0.02	0.03	0.00	0.52	0.52
60 to 75°N	HRBM	0.08	2.01	2.74	4.75	4.73	21.62	26.35
	FBM	0.18	6.80	4.74	11.54	19.78	34.79	54.75
	TEM	0.07	1.00	2.60	3.60	0.32	26.00	26.32
45 to 60°N	HRBM	0.18	5.03	6.31	11.34	12.85	49.36	62.21
	FBM	0.38	13.93	6.50	20.43	49.06	55.37	104.43
	TEM	0.10	2.20	3.50	5.70	1.70	25.60	27.30
30 to 45°N	HRBM	0.15	3.65	5.45	9.10	9.90	36.21	46.11
	FBM	0.23	8.48	4.81	13.29	27.92	29.68	57.60
	TEM	0.11	3.09	3.31	6.40	3.90	15.71	19.61
15 to 30°N	HRBM	0.15	4.05	5.14	9.19	10.47	28.71	39.18
	FBM	0.22	7.96	2.93	10.89	20.15	20.87	41.02
	TEM	0.09	4.35	2.81	7.16	3.31	7.75	11.06
0 to 15°N	HRBM	0.25	9.03	6.89	15.92	25.29	32.81	58.10
	FBM	0.38	15.37	4.56	19.93	38.43	25.42	63.85
	TEM	0.12	12.27	5.63	17.90	2.83	9.28	12.11
15 to 0°S	HRBM	0.32	13.26	7.36	20.62	40.23	36.56	76.79
	FBM	0.61	24.55	7.49	32.04	61.06	43.09	104.15
	TEM	0.12	15.36	6.54	21.90	2.84	10.94	13.78
30 to 15°S	HRBM	0.13	3.87	4.48	8.35	10.41	21.53	31.94
	FBM	0.18	6.07	3.78	9.85	16.34	24.11	40.45
	TEM	0.12	4.51	3.54	8.05	2.74	8.83	11.57
45 to 30°S	HRBM	0.05	1.59	1.63	3.22	4.22	10.31	14.53
	FBM	0.05	1.64	0.93	2.57	4.74	8.80	13.54
	TEM	0.03	0.74	1.10	1.84	0.71	4.05	4.76
60 to 45°S	HRBM	0.01	0.20	0.26	0.46	0.52	2.02	2.54
	FBM	0.01	0.23	0.14	0.37	0.56	1.05	1.61
	TEM	0.00	0.09	0.18	0.27	0.13	0.96	1.09

changes in total carbon storage estimated by the spatially explicit models reflect the latitudinal distribution of NEP in 1990 (Table 3). For TEM, the historical change in total carbon storage in tropical regions is relatively higher than that indicated by NEP in these regions during 1990. In addition, most of this carbon has accumulated in areas covered by tropical rain forests (Fig. 5) rather than the drier areas described before. This result occurs because NEP estimated by TEM in tropical regions was much larger during the early 1900s than during 1990 (Fig. 6). The FBM estimates that most of the accumulated carbon is stored in vegetation over all latitudes whereas HRBM and TEM estimate that most of the carbon accumulated outside of tropical regions is stored in soils (Tables 2 and 3). At the global scale, the Bern model estimates that the additional carbon is stored almost equally between vegetation (45%) and soils (55%).

3.2. *Response of the terrestrial biosphere to projected changes in atmospheric CO$_2$ concentration*

In all models, estimates of both annual NPP and annual R_H continue to increase over time (Fig. 3a) in response to the projected increases in atmospheric CO$_2$ concentration under the IPCC S650 profile. From 1990 to 2300, the models estimate that annual NPP increases by 1.1 to 10.4 Pg C yr^{-1} and that annual R_H increases by

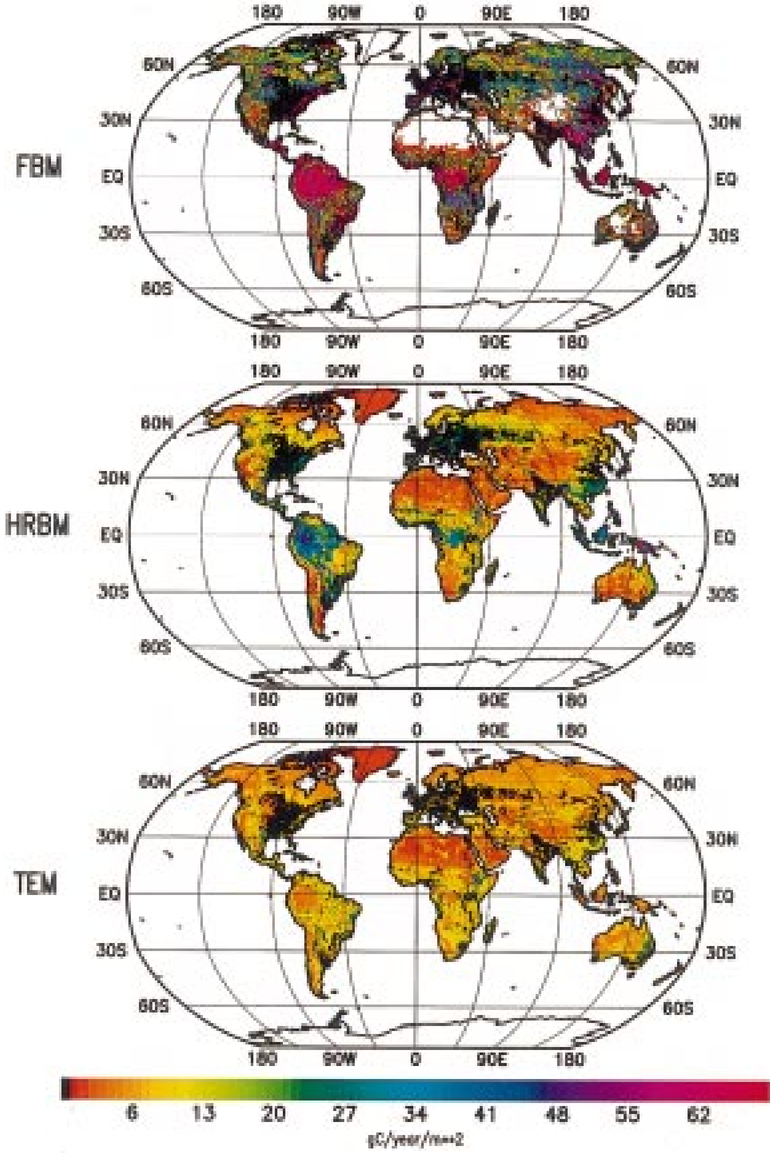

Fig. 4. Comparison of the spatial distribution of net ecosystem productivity (g C m^{-2} yr^{-1}) in natural areas during 1990 among the spatially explicit models (FBM, HRBM, TEM).

1.8 to 11.4 Pg C yr^{-1} (Table 2). The Bern model estimates the largest absolute increases in NPP and R_H whereas FBM estimates the largest relative increases in NPP (+23.4%) and R_H (+29.8%). The TEM estimates the smallest relative and absolute increases in NPP (+3.2%) and R_H (+5.4%).

Unlike the historical period, however, the relative relationship between annual estimates of NPP and R_H changes in all the projections of carbon fluxes by the models. At first, annual R_H lags the comparable increase in annual NPP so that NEP continues to increase over time for all models (Fig. 3b). Then, the stabilization of atmospheric

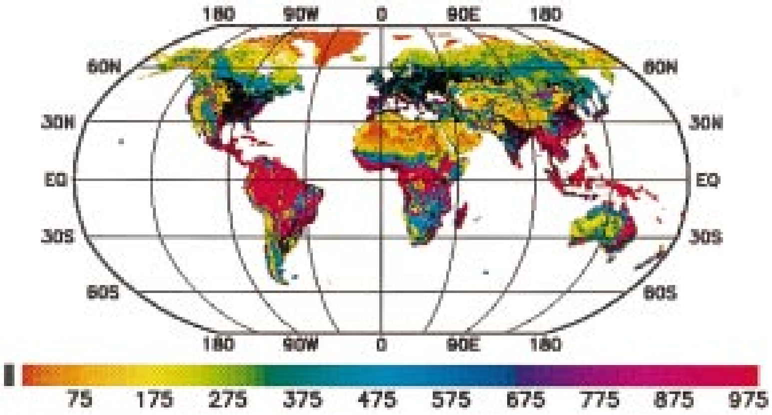

Fig. 5. The spatial distribution of carbon accumulation ($g\,C\,m^{-2}\,yr^{-1}$) in natural areas estimated by TEM from 1765 to 1990.

CO_2 causes a comparable stabilization of NPP and R_H such that NEP is close to zero and little or no additional atmospheric CO_2 is being stored in terrestrial ecosystems by the year 2300. These NEP results suggest that terrestrial ecosystems have a limited and time-dependent ability to sequester carbon in the future if atmospheric CO_2 concentrations become stable.

Although the projected increases in NEP after 1990 by all the models (Table 2) suggest that more carbon can be stored in terrestrial ecosystems as a result of CO_2 fertilization, the models differ on the amount of carbon that can be sequestered in the future. From 1990 to 2300, the FBM estimates the largest increase (481 Pg C) in carbon storage in natural areas whereas TEM estimates the smallest increase (126 Pg C). The low estimate of carbon accumulation by TEM is a result of carbon uptake being tightly constrained by nitrogen availability in TEM. The Bern model estimates that 436 Pg C accumulates in both natural and disturbed areas.

In addition, the models differ in how carbon is stored in terrestrial ecosystems across the globe after 1990 (Fig. 6; Table 3). The change in total carbon storage in the tropics between 1990 and 2300 is three to four times that estimated between 1765 and 1990 for FBM and HRBM. The projected change in tropical carbon storage for TEM, however, is only 60 to 70% of that estimated between 1765 and 1990. Relatively larger changes in total carbon storage are projected for the northern temperate/boreal regions by all the spatially explicit models where estimates are 4 to 6 times larger than the historical change in total carbon. As a result, TEM estimates that more carbon is added to northern temperate/boreal regions than to the tropics after 1990. The FBM estimates that about equal amounts of carbon are added to northern temperate/boreal and tropical regions. Only HRBM estimates that more carbon is still added to the tropics than the northern temperate/boreal regions.

The shift of the major terrestrial carbon sink from tropical regions to the northern temperate/boreal region estimated by TEM (Fig. 6) is caused by nitrogen limitation of tropical NPP as a result of the closed nitrogen cycle during the transient simulation by TEM (Tian et al., this issue). In contrast to the historical changes in carbon storage, a larger proportion of the additional carbon is estimated to be stored in soils rather than vegetation in the future by all the models (Table 2). In the tropics, 41 to 79% of future additional carbon is estimated to be stored in soils as compared to 23 to 36% of the carbon added historically by the spatially explicit models (Table 3). In the northern temperate/boreal region, 53 to 94% of future additional carbon is estimated to be stored in soils by the spatially explicit models. The FBM estimates the smallest proportion of additional carbon that will be stored in soils whereas TEM estimates the largest proportion.

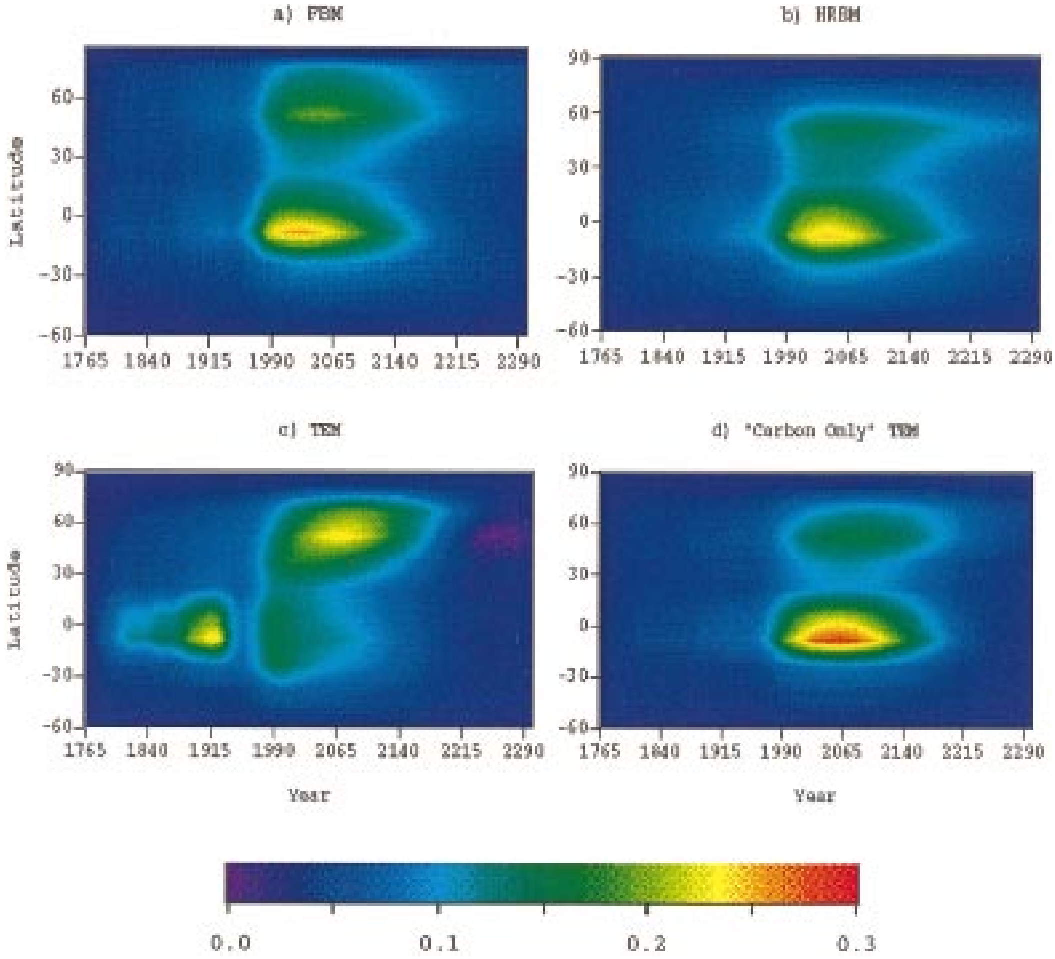

Fig. 6. Comparison of interannual variations in the latitudinal distribution of net ecosystem productivity (NEP) among three of the terrestrial biosphere models (FBM, HRBM, TEM) and the "carbon only" version of TEM between 1765 and 2300. Model estimates have been normalized to the maximum global NEP estimated by the corresponding model. We normalized by dividing the resulting latitudinal NEP estimates of each model by the maximum global NEP determined over the study period (1765 to 2300) by the same model (see previous section) to examine the relative changes in NEP over time and space.

3.3. *Variations in the sensitivity of NPP to CO_2 fertilization among the terrestrial biosphere models*

The sensitivity of simulated NPP to CO_2 fertilization varies among the models over time and space as a result of the different approaches used to simulate the influence of atmospheric CO_2 on NPP. Because the Bern model uses a constant β factor, the sensitivity of simulated NPP to CO_2 fertilization does not change over time. In contrast, the sensitivity of simulated NPP to CO_2 fertilization, as represented by the "effective" β_{LOG} (Table 4), decreases from 1990 to 2300 in the simulations of FBM, HRBM and TEM. As a result, the historical NPP estimates of the Bern model are less sensitive to CO_2 fertilization than the comparable NPP estimates of all the spatially explicit models, but the future estimates of NPP are more sensitive to CO_2 fertilization than comparable NPP estimates of TEM. Among the spatially explicit models, the NPP estimates of FBM

Table 4. *Comparison of "effective" β_{LOG} factors estimated by the terrestrial biogeochemistry models for the years 1990 to 2300*

Year	Bern	HRBM	FBM	TEM
1990				
tropical	—	0.525	0.666	0.459
extratropical	—	0.603	0.984	0.234
total	0.289	0.548	0.771	0.382
2050				
tropical	—	0.436	0.550	0.259
extratropical	—	0.496	0.862	0.199
total	0.284	0.453	0.653	0.239
2200				
tropical	—	0.332	0.459	0.176
extratropical	—	0.397	0.724	0.100
total	0.286	0.350	0.546	0.150
2300				
tropical	—	0.332	0.454	0.176
extratropical	—	0.397	0.734	0.100
total	0.286	0.350	0.546	0.150

are always the most sensitive to CO_2 fertilization (i.e., the largest effective β_{LOG} values) and the NPP estimates of TEM are always the least sensitive to CO_2 fertilization (i.e., the smallest effective β_{LOG} values). The high sensitivity of NPP to CO_2 fertilization estimated by FBM appears to be caused by corresponding increases in leaf area. The low sensitivity of NPP to CO_2 fertilization estimated by TEM is caused by nitrogen limitation of NPP assumed in the model.

The results of the spatially explicit models also suggest that the sensitivity of NPP to CO_2 fertilization varies across the globe, but the models disagree on the location of the regions with the greatest sensitivity. According to FBM and HRBM, simulated NPP in extra-tropical regions is more sensitive to CO_2 fertilization than NPP in tropical regions whereas TEM estimates that NPP in tropical regions is more sensitive to CO_2 fertilization. Nitrogen is generally assumed by TEM to be more available for plant growth in tropical regions than extra-tropical regions so that NPP is not as constrained in tropical regions (Melillo et al., 1993; McGuire et al., 1997; Xiao et al., 1997, 1998).

3.4. *Variations in the response of carbon storage to CO_2 fertilization among the terrestrial biosphere models*

In addition to increased NPP, carbon sequestration in terrestrial ecosystems depends on the ability of the ecosystems to retain carbon. By calculating mean residence times of carbon in various terrestrial pools, we examine how differences in the representation of terrestrial carbon storage among the models (Table 1) may have influenced the simulated ability of terrestrial ecosystems to retain carbon. Estimates of mean residence times for carbon in the terrestrial biosphere (τ_{TOTAL}) derived from HRBM estimates are about twice as long as those derived from estimates of the Bern model, FBM and TEM over the study period (Table 5). In addition to this result, a comparison of the estimates of τ_{TOTAL} to corresponding estimates of the mean residence times of carbon added to the terrestrial biosphere since 1765 or "excess carbon" (τ_{EX}) suggests that the carbon stock estimates of the Bern model, FBM and TEM include mostly biologically reactive carbon whereas the HRBM estimates include stocks of more refractory carbon.

Unlike the model estimates of τ_{TOTAL} which remained fairly constant from 1990 to 2300, estimates of τ_{EX} increase with time for all models suggesting that carbon added to the terrestrial biosphere in the future will reside in terrestrial ecosystems longer than past accumulations of carbon in the absence of human or natural disturbances. The largest change in τ_{EX} (20.2 years) is derived from the estimates of HRBM whereas the smallest change in τ_{EX} (9.1 years) is derived from the FBM estimates. Overall, "excess carbon" spends the least amount of time in the terrestrial biosphere in the simulations of the Bern model (τ_{EX} ranges from 24.2 to 35.4 years) and the longest amount of time in the TEM simulations (τ_{EX} ranges from 34.7 to 51.8 years).

Since the mean residence times of excess vegetation carbon (τ_{VEG}) derived from the estimates of the various models remain relatively constant from 1990 to 2300 (Table 5), the temporal changes in τ_{EX} reflect similar changes in the mean residence times of excess soil organic carbon (τ_{SOIL}). Values of τ_{SOIL} in tropical regions are less than those estimated for extra-tropical regions for all models (Table 5) because environmental conditions in the warmer tropics are generally more suitable for high rates of decomposition, which decrease stocks of soil organic matter, than the cooler regions outside of the tropics.

Similar to Thompson et al. (1996), our results suggest that the size of a terrestrial carbon sink

Table 5. *Comparison of mean residence times (years) for total carbon storage (τ_{TOTAL}), the storage of carbon added to the terrestrial biosphere after 1765 (τ_{EX}), excess vegetation carbon (τ_{VEG}) and excess soil (τ_{SOIL}) derived from the estimates of the terrestrial biosphere models for years 1990 to 2300*

	τ_{TOTAL}				τ_{EX}				τ_{VEG}				τ_{SOIL}			
Year	Bern	HRBM	FBM	TEM	Bern	HRBM	FBM	TEM	Bern	HRBM	FBM	TEM	Bern	HRBM	FBM	TEM
1990																
tropical	—	33.6	25.7	25.8	—	18.5	32.3	29.9	—	4.9	21.0	17.5	—	12.1	8.3	10.1
extratropical	—	123.6	40.9	58.4	—	59.0	29.1	67.1	—	39.3	16.4	14.4	—	20.8	10.3	40.2
total	36.4	59.5	30.9	36.4	24.2	30.1	30.9	34.7	8.9	12.7	19.1	16.9	13.3	14.6	9.2	13.9
2050																
tropical	—	33.0	26.5	26.1	—	21.1	33.3	30.4	—	5.7	21.7	16.7	—	14.1	9.2	13.4
extratropical	—	118.5	40.1	59.1	—	65.1	31.9	88.6	—	38.5	18.6	18.6	—	24.0	11.1	57.2
total	35.8	58.0	31.3	36.9	25.4	34.0	32.7	40.7	9.3	14.3	20.4	17.1	14.3	17.0	10.0	20.7
2200																
tropical	—	33.8	28.2	26.5	—	28.7	36.5	33.8	—	7.1	21.8	15.6	—	21.2	13.9	18.0
extratropical	—	119.1	41.7	62.8	—	86.6	40.1	118.1	—	39.6	20.0	15.7	—	42.1	18.9	98.1
total	36.2	58.7	33.1	38.2	32.6	46.1	38.0	51.8	10.0	17.2	21.1	15.7	21.9	27.5	16.0	35.1
2300																
tropical	—	34.2	28.4	26.5	—	30.9	37.5	33.7	—	7.3	21.9	15.6	—	23.5	15.4	18.0
extratropical	—	121.0	42.1	62.3	—	118.9	43.5	108.8	—	40.0	20.0	15.7	—	51.1	22.8	93.3
total	36.7	59.5	33.8	38.1	35.4	50.3	40.0	50.6	10.0	17.7	21.1	15.7	25.2	31.9	18.6	35.0

estimated by the models depends on initial NPP, the strength of the CO_2 fertilization effect on NPP, and the mean residence time of carbon in the terrestrial biosphere. We find that model assumptions about the strength of the CO_2 fertilization effect on NPP have the largest influence on the estimated size of the terrestrial carbon sink. However, our results do suggest that the initial NPP rates and mean residence times still play a role in determining the size of terrestrial sinks. Although the Bern model uses a β factor that is smaller than the comparable effective β_{LOG} factors calculated from HRBM (Table 4), it estimates a similar terrestrial sink (Fig. 3b; Table 2). The high initial NPP estimate by the Bern model appears to compensate for the relatively low sensitivity of NPP to CO_2 fertilization when determining the size of the terrestrial carbon sink. In addition, the relatively high rates of carbon accumulation in tropical ecosystems estimated by FBM and HRBM are influenced more by the high NPP rates generally occurring in tropical ecosystems than by the relatively lower sensitivity of NPP to CO_2 fertilization (Table 4). As the effective β_{LOG} factors determined from the models in this study decreased and τ_{EX} increased with the stabilization of atmospheric CO_2, the ability of terrestrial ecosystems to retain carbon may become more of an important factor for sustaining terrestrial carbon sinks in the future.

4. Discussion

In many past studies that explored the potential role of CO_2 fertilization on the global carbon cycle, all terrestrial ecosystems in the world have typically been treated as a single entity with only a single response to CO_2 fertilization. This response has most often been simulated with a constant β factor and turnover time where changes in terrestrial carbon storage are assumed to be proportional to changes in atmospheric CO_2 concentration from contemporary conditions. Recently, improvements in computer technology and the availability of spatially explicit data sets on a variety of environmental variables have allowed the development of a new family of terrestrial biosphere models that include fundamental processes of ecophysiology and biogeochemistry. These models can consider the influence of spatial and temporal variations in environmental factors on the spatially specific uptake and storage of carbon in terrestrial ecosystems. The new models differ in complexity and emphasize different ecosystem processes (Cramer et al., in press). These model differences result in a range of estimates of the effects of CO_2 fertilization on terrestrial carbon fluxes and storage.

The results of our study give us insight into why the range exists and what kind of things we need to do to reduce the range. In this section, we begin by looking at the implications of the simulated responses of terrestrial carbon fluxes and stocks to historical and future changes in atmospheric CO_2 concentrations. We then identify issues where additional research and data would help to reduce uncertainties in future modeling studies.

Although the NEP estimates of all the models used in this study indicate the potential importance of CO_2 fertilization as a mechanism for explaining a part of the missing carbon sink, an analysis of the model results suggests that other factors are also influencing the missing carbon sink on land. These factors include the effects of nitrogen limitation and fertilization, climate change and the regrowth of forests after disturbance.

In this study, models that did not consider the influence of nutrient limitations on NPP (the Bern model, FBM) estimate more storage of carbon in terrestrial ecosystems during the historical period than the models that did consider the influence of nutrient limitations on NPP (HRBM, TEM). As NPP in many terrestrial ecosystems is known to be limited by nitrogen availability (Melillo and Gosz, 1983; Vitousek and Howarth, 1991; Melillo, 1995; Schimel 1995), the models that do not consider nutrient limitations probably overestimate the response of terrestrial carbon storage to CO_2 fertilization. To explore this further, we did an additional experiment with TEM. We parameterized TEM such that carbon fluxes are not constrained by the nitrogen cycle, i.e., nitrogen is always sufficiently available for optimal plant growth. This "carbon only" version of TEM estimates a higher NEP (3.5 Pg C yr^{-1} in 1990; see red dashed line in Fig. 3b). In addition, the pattern of relative NEP over space and time estimated by the "carbon only" version of TEM is similar to that of FBM and HRBM (Fig. 6d).

A comparison of the results from TEM to the "carbon only" version of TEM suggests that incorporating the effect of nitrogen fertilization on terrestrial ecosystems will cause TEM to estimate a higher NEP than is provided by CO_2 fertilization alone. This result is consistent with the results of other studies that suggest that terrestrial carbon storage increases as a result of nitrogen fertilization (Melillo and Gosz, 1983; Peterson and Melillo, 1985; Schindler and Bayley, 1993; Hudson et al., 1994; Townsend et al., 1996; Holland et al., 1997).

Recent studies (Dai and Fung, 1993; Braswell et al., 1997; Tian et al., 1998; Tian et al., this issue) suggest that interannual variations in climate have affected historical and contemporary carbon stocks and fluxes from terrestrial ecosystems. As this study used a long-term mean climate as inputs during the model simulations, we were not able to assess the effects of climate change or interannual climate variability on past or future terrestrial carbon storage. However, the spatial variations in the simulated response of terrestrial ecosystems to CO_2 fertilization by the spatially explicit models suggest that climate conditions may restrict the ability of terrestrial ecosystems to sequester carbon during certain times of the year. Although NPP is nitrogen-limited in many northern ecosystems, unfavorable climate conditions, particularly during the winter or dry season, also restrict the benefits of CO_2 fertilization to terrestrial carbon storage in these areas (Xiao et al., 1998; Tian et al., this issue). This result suggests that climate changes associated with enhanced atmospheric CO_2 concentrations, i.e., the so-called "greenhouse effect," will also have an influence on the ability of terrestrial ecosystems to sequester carbon in northern ecosystems. A cursory comparison of NPP and NEP in tropical versus extra-tropical regions suggests that temperature increases in northern ecosystems would result in enhanced carbon sequestration, but associated changes in the spatial and temporal patterns of evapotranspiration and precipitation may restrict the benefits of CO_2 fertilization on plant productivity due to moisture limitations. Even in tropical rain forests, where contemporary climate conditions are generally considered optimal, the uptake of carbon may be restricted by seasonal changes in precipitation (Tian et al., 1998). In addition, seasonal changes in solar radiation at middle to high latitudes will not change with climate change, with the exception of cloud cover, so that NPP and the effects of CO_2 fertilization will always be restricted in these areas during some parts of the year (see also Kicklighter et al., in press).

In this first-order analysis, we did not explicitly consider the effects of reforestation or forest regrowth after harvest on the terrestrial carbon sink. For the spatially explicit models, we assumed that CO_2 fertilization increases carbon storage only in natural areas. As vegetation is now being allowed to grow in many areas formerly used for agriculture, CO_2 fertilization, nitrogen fertilization and climate change may be causing vegetation and soils to store more carbon in these disturbed areas than is being attributed in current carbon budgets. Because the ability of forests to accumulate carbon varies with age, the influence of CO_2 fertilization, N fertilization and climate change on forest regrowth will change over time. In addition, the influence of natural disturbances, such as fires or hurricanes, on terrestrial carbon dynamics has not been explicitly considered by any of the model simulations in this study. Climate change may also influence the severity or frequency of these disturbances. Thus, a comprehensive analysis of CO_2 fertilization on terrestrial carbon storage should include the rôle of disturbances in shaping the structure and function of ecosystems to gain a better understanding of global carbon dynamics (Houghton et al., 1983, 1987; Esser, 1987; Melillo et al., 1988, 1996a; Houghton, 1991, 1995; Hall and Uhlig, 1991; Dixon et al., 1994; Kurz et al., 1995a, 1995b).

Although synergetic effects among CO_2 concentration, nitrogen deposition, climate and forest regrowth may enhance the uptake of atmospheric carbon by terrestrial ecosystems, acclimation of terrestrial ecosystems to new environmental conditions may reduce the influence of these factors on carbon sequestration. This acclimation is not fully understood in detail and has not been explicitly considered in the modeling experiment presented here although the TEM response to nitrogen limitation may represent such an acclimation response (McGuire et al., 1997). Thus, the total effect of these factors on terrestrial carbon storage should include the effects of interactions among the carbon and nitrogen cycles, climate, and the influence of human and natural disturbances on terrestrial ecosystems.

Clearly, these multiple and interacting mechanisms will affect carbon storage in the future. Perhaps the most important will be changes in land use. Our single factor analysis of CO_2 fertilization, however, does say something very important about the future capacity of terrestrial ecosystems to sequester carbon. Our analysis suggests that terrestrial carbon storage can increase as a result of CO_2 fertilization, but it also suggests that terrestrial ecosystems have a limited ability to sequester carbon by this mechanism in a stabilization scenario. How long would terrestrial ecosystems continue to store carbon if the atmospheric CO_2 concentration were not stabilized? Are there physiological limits to CO_2 fertilization? If yes, are they general or species specific? Our analysis addresses some of these questions.

Changes in the size and location of the terrestrial sinks estimated by each of the terrestrial models are primarily related to comparable changes in NPP. Model estimates of the terrestrial sink are large during time periods when NPP is increasing rapidly and become diminished if NPP rates become more stable. As all the models use functions that assume the relative enhancement of NPP decreases with higher atmospheric CO_2 concentrations, all the models suggest that there is a physiological limit to the amount of carbon that terrestrial ecosystems will be able to store even if atmospheric CO_2 concentrations continue to increase. Furthermore, the TEM results indicate that additional storage of carbon may be even more restricted by nutrient constraints on NPP. The FBM results, however, suggest that changes in vegetation structure related to changes in leaf area may increase the sink capacity of terrestrial ecosystems for anthropogenic carbon.

Although the models in this study collectively include the most important mechanisms for simulating the effects of CO_2 fertilization on terrestrial carbon storage, no one model contains all of the important mechanisms influencing how carbon is sequestered in terrestrial ecosystems. Instead the models emphasized the role of different mechanisms on the uptake and storage of carbon in terrestrial ecosystems (see also Pan et al., 1998). For example, changes in leaf area with increasing CO_2 concentration indirectly enhanced the effect of CO_2 fertilization in the FBM simulations whereas changes in relative nitrogen availability with increasing CO_2 concentration restricted the benefits of CO_2 fertilization in TEM simulations. These differences caused large differences in the simulated response of natural terrestrial ecosystems to CO_2 fertilization.

Our study points to a small number of high priority research needs that must be met to improve our understanding of the capacity of terrestrial ecosystems to store carbon. These needs can be divided into three categories: (1) better spatially explicit data of important environmental factors for model input; (2) more field observations, both local and global; (3) more whole-ecosystem experiments. The development of historical data sets that describe the spatial and temporal changes in land use, land cover, climate, and nitrogen deposition at fine spatial and temporal resolutions are needed to help improve regional estimates of the effects of CO_2 fertilization on the terrestrial biosphere.

Desired observational data include both site-specific measures of net carbon exchange and well constrained global indexes that will allow us to calculate large fluxes of carbon between land and that atmosphere at continental scales, latitudinal bands, etc. Unlike the previous generation of models, the spatially explicit estimates of the newer models can also be compared against field measurements of carbon stocks and fluxes at specific sites across the globe to help evaluate the credibility of these new models. Recently, field measurements of carbon fluxes (e.g., net ecosystem exchange, gross ecosystem exchange) at finer temporal resolutions have become available (Wofsy et al., 1988, 1993; Fan et al., 1990; Gao, 1994; Grace et al., 1995, 1996; Baldocchi et al., 1996; Black et al., 1996; Goulden et al., 1996, 1998; Greco and Baldocchi, 1996; Valentini et al., 1996; Miranda et al., 1997), but these data exist only for a limited number of sites and for very short time periods. The development of a network of sites measuring net carbon exchange and concurrent environmental conditions across the globe (Kaiser, 1998) should help to improve our ability to calibrate models and evaluate future model results. At larger spatial scales, the calculation of the ratio of atmospheric N_2 to O_2 measured at a network of sites across the globe helps to identify the relative contribution of oceans and the terrestrial biosphere to the missing carbon sink and how this sink is distributed across the globe (Bender et al., 1996; Keeling et al., 1996).

Terrestrial ecosystems are complex, non-linear systems with many feedback mechanisms that influence the size and the timing of the responses of these systems to CO_2 fertilization. Within a plant community, the response of various species to CO_2 fertilization may vary such that some plants may become larger or more abundant whereas other plants may be unaffected (Owensby et al., 1993, 1995). Interactions with the soil microbial community may also affect the response of a plant community to CO_2 fertilization by influencing nitrogen availability (Hungate et al., 1997a). As a result, the response of an ecosystem to CO_2 fertilization cannot be determined solely from laboratory or field studies based on one or two plant species (McGuire et al., 1995). Whole-ecosystem experiments are needed. Because of the "greenhouse effect," a key experiment may be to examine the combined effects of enhanced CO_2 and enhanced temperatures on forest ecosystems in facilities such as Biosphere II. This experiment should be conducted to integrate information about the responses of various plant and soil organisms with information about ecosystem-scale changes such as community metabolism. These results could then be used to evaluate if the appropriate mechanisms are being used in a model to simulate the response of an ecosystem process to CO_2 fertilization.

As atmospheric CO_2 concentrations are likely to continue to increase, we need to understand how terrestrial ecosystems will respond to enhanced atmospheric CO_2 concentrations and associated climate changes. This study has provided some insights into the potential role of CO_2 fertilization on the sequestration of anthropogenic carbon in terrestrial ecosystems, but there is much yet to learn. With improvements in future input data sets and the availability of measurements from new field studies of net carbon exchange and whole-ecosystem experiments to check model assumptions and results, spatially explicit terrestrial biosphere models can be used as a tool in the future to improve our understanding of the role of CO_2 fertilization on terrestrial carbon storage.

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