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Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land use effects with four process-based ecosystem models

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Abstract. The concurrent effects of increasing atmospheric CO_2 concentration, climate variability, and cropland establishment and abandonment on terrestrial carbon storage between 1920 and 1992 were assessed using a standard simulation protocol with four process-based terrestrial biosphere models. Over the long-term (1920-1992), the simulations yielded a time history of terrestrial uptake that is consistent (within the uncertainty) with a long-term analysis based on ice core and atmospheric CO_2 data. Up to 1958, three of four analyses indicated a net release of carbon from terrestrial ecosystems to the atmosphere caused by cropland establishment. After 1958, all analyses indicate a net uptake of carbon by terrestrial ecosystems, primarily because of the physiological effects of rapidly rising atmospheric CO_2. During the 1980s the simulations indicate that terrestrial ecosystems stored between 0.3 and 1.5 Pg C yr^{-1}, which is within the uncertainty of analysis based on CO_2 and O_2 budgets. Three of the four models indicated (in accordance with O_2 evidence) that the tropics were approximately neutral while a net sink existed in ecosystems north of the tropics. Although all of the models agree that the long-term effect of climate on carbon storage has been small relative to the effects of increasing atmospheric CO_2 and land use, the models disagree as to whether climate variability and change in the twentieth century has promoted carbon storage or release. Simulated interannual variability from 1958 generally reproduced the El Niño/Southern Oscillation (ENSO)-scale variability in the atmospheric CO_2 increase, but there were substantial differences in the magnitude of interannual variability simulated by the models. The analysis of the ability of the models to simulate the changing amplitude of the seasonal cycle of atmospheric CO_2 suggested that the observed trend may be a consequence of CO_2 effects, climate variability, land use changes, or a combination of these effects. The next steps for improving the process-based simulation of historical terrestrial carbon include (1) the transfer of insight gained from stand-level process studies to improve the sensitivity of simulated carbon storage responses to changes in CO_2 and climate, (2) improvements in the data sets used to drive the models so that they incorporate the timing, extent, and types of major disturbances, (3) the enhancement of the models so that they consider major crop types and management schemes, (4) development of data sets that identify the spatial extent of major crop types and management schemes through time, and (5) the consideration of the effects of anthropogenic nitrogen deposition. The evaluation of the performance of the models in the context of a more complete consideration of the factors influencing historical terrestrial carbon dynamics is important for reducing uncertainties in representing the role of terrestrial ecosystems in future projections of the Earth system.

1. Introduction

The development of an improved understanding of terrestrial carbon dynamics is taking on increased political and scientific importance [*Melillo et al.,* 1996; *Schimel et al.,* 1996]. For the past three decades, terrestrial carbon cycle research has addressed fundamental problems in Earth System Science. Given the atmospheric CO_2 record, could we account for its seasonal and interannual patterns [*Keeling and Revelle,* 1985; *Keeling et al.,* 1995] and the apparent existence of terrestrial sinks that have moderated the rate of accumulation of CO_2 [*Tans et al.,* 1990; *Denning et al.,* 1995, 1999; *Heimann and Kaminski,* 1999; *Rayner et al.,* 1999]? With the development of ice-core records of CO_2 [*Etheridge et al.,* 1996; *Indermuehle et al.,* 1999; *Smith et al.,* 1999; *Petit et al.,* 1999], could we account for natural variations of CO_2 concentration that seem to be associated with climate change on longer timescales [Bruno and Joos, 1997]? These questions, still only partially answered, have taken on additional importance and urgency in the wake of the United

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Nations climate conference in Kyoto (Framework Convention on Climate Change available at http://www.unfccc.de/resource/cop3.html). Articles 3.3 and 3.4 of the Kyoto Protocol set targets for limiting emissions of greenhouse gases and allowed for active management of the terrestrial biosphere as a complementary measure to emissions reductions (Framework Convention on Climate Change available at http://www.unfccc.de/resource/cop3.html). Locating the sources and sinks for CO_2 and understanding them well enough to predict how they will respond to deliberate management or to inadvertent climate change have emerged as major international policy issues, with potentially immense economic implications [*Wigley et al.,* 1996].

The major components of the atmospheric carbon budget on the timescale of human lifetimes are fossil-fuel CO_2 emissions, exchanges of CO_2 between the ocean and the atmosphere, and exchanges of CO_2 between the terrestrial biosphere and the atmosphere [*Schimel et al.,* 1996]. The net carbon exchange (NCE) between the terrestrial biosphere and the atmosphere can be described by the equation:

$$\mathrm{NCE} = R_H - \mathrm{NPP} + E_{\mathrm{NAD}} + E_{AD} + E_P, \quad (1)$$

where R_H is heterotrophic respiration (i.e., decomposition), NPP is net primary production, E_{NAD} represents emissions associated with nonanthropogenic disturbance, E_{AD} represents emissions from anthropogenic disturbance, and E_P represents the decomposition of products harvested from ecosystems for human use. A positive NCE indicates a terrestrial source of atmospheric CO_2, whereas a negative NCE indicates a terrestrial sink. The fluxes NPP and R_H represent production and decomposition of organic matter in land-based and fresh-water aquatic ecosystems of the terrestrial biosphere and are influenced by changes in atmospheric CO_2, variability and changes in climate, disturbance history, and the deposition of anthropogenic nitrogen [*Schimel et al.,* 1996, 1997, 2000]. Also, the flux R_H includes decomposition of carbon that is transported from one location to another in the terrestrial biosphere through runoff, leaching, and other erosion processes as dissolved inorganic carbon, dissolved organic carbon, and particulate organic carbon [*Kling et al.,* 1991; *Stallard,* 1998; *Harden et al.,* 1999]. In addition to exchange with the atmosphere, the terrestrial biosphere also exports carbon in river inputs to the oceans, much of which is decomposed and released back to the atmosphere in estuary and coastal marine environments [*Schlesinger,* 1991]. Terrestrial biosphere-atmosphere exchanges are also influenced by emissions associated with nonanthropogenic disturbances, for example, fires caused by lightning, as well as anthropogenic disturbances, which include clearing of land for agriculture, conversion of forest to pasture, and the harvest of forest products. The products harvested from agriculture and forestry may also be transported from one location to another and decompose at locations far from the site of harvest.

Cropland establishment and abandonment is an important anthropogenic influence on terrestrial biosphere-atmosphere exchanges. The clearing of land for agriculture contributes significantly to CO_2 emissions, and abandonment of agriculture and subsequent forest management can contribute significantly to CO_2 uptake [*Houghton,* 1999]. On average during the 1980s, of 5.5 Pg C yr^{-1} that were released to the atmosphere as CO_2 because of fossil fuel burning, only 3.3 Pg C yr^{-1} remained in the atmosphere. According to the 1995 analysis of the Intergovernmental Panel on Climate Change (IPCC), 2.0 Pg C yr^{-1} were taken up by the ocean while the terrestrial biosphere was approximately neutral [Schimel et al., 1996]. That is, the carbon source from the biosphere due to land use change, mainly in the tropics (estimated at 1.6 Pg C yr^{-1}), was approximately balanced by sinks (estimated at 1.8 Pg C yr^{-1}) in other terrestrial ecosystems. A recent reanalysis of the land use contribution by *Houghton* [1999] has yielded a slightly larger estimate of the anthropogenic source of 2.0 Pg C yr^{-1}, implying a somewhat larger terrestrial biosphere sink. The terrestrial biosphere has also been estimated to deliver between 0.4 and 0.5 Pg C yr^{-1} in river inputs to the ocean [*Schlesinger,* 1991].

The contribution of land use changes to the global CO_2 budget has traditionally (as given by *Schimel et al.* [1996]) been estimated with bookkeeping models [*Houghton et al.,* 1983; *Houghton,* 1999] that balance deforestation and forest regrowth over time, assuming generic time-dependent functions for carbon gains and losses in different ecosystem types. Of the land use changes considered in an analysis by *Houghton* [1999], cropland establishment/abandonment was responsible for 68% of the net land use flux, while harvest of wood, conversion of forests to pastures, and shifting cultivation accounted for 16, 13, and 4% of the net flux, respectively. Several mechanisms were proposed by *Schimel et al.* [1996] to explain the terrestrial uptake that is required to balance land use emissions computed in this way. These mechanisms included physiological responses of terrestrial ecosystems to increasing ambient CO_2 concentrations and anthropogenic N deposition and variations in productivity due to climate variability. An additional contribution to terrestrial carbon uptake was ascribed, more controversially, to forest regrowth in northern extratropical ecosystems. Recently, the net carbon storage associated with physiological mechanisms has been independently estimated in a number of different process-based model analyses that have evaluated the effects of rising atmospheric CO_2 [*Kicklighter et al.,* 1999a], climate variability [*Kindermann et al.,* 1996; *Braswell et al.,* 1997], rising CO_2 and climate [*Tian et al.,* 1998, 1999a, 1999b, 2000; *Cao and Woodward,* 1998; *Meyer et al.,* 1999; *McGuire et al.,* 2000a], and anthropogenic N deposition [*Townsend et al.,* 1996; *Holland et al.,* 1997; *Nadelhoffer et al.,* 1999; *Lloyd,* 1999]. The analyses suggest that each of these mechanisms could be playing a significant role in the global CO_2 budget. It is quite conceivable that their combined effects could counterbalance the net release of carbon associated with land use change. However, a rigorous analysis has not been possible because the various proposed mechanisms are by no means independent. For example, the effects of CO_2 and N deposition may be synergistic [*Lloyd,* 1999], and the effects of CO_2 and climate interact [*Long,* 1991]. There is also widespread confusion about what effects are included in the traditional estimates of the land use contribution [*Kauppi et al.,* 1992a, 1992b; *Rastetter and Houghton,* 1992] and indeed there may be strong interactions between the regrowth component and the other mechanisms. For example, the effects of rising CO_2 in forests may be strongest during regrowth in which faster early growth leads to faster canopy development and higher photosynthesis. Thus the positive and negative sides of the terrestrial carbon balance may be confounded between analyses that do not simultaneously consider the major factors influencing changes in terrestrial carbon storage.

The net exchange of carbon between the atmosphere and terrestrial ecosystems has not previously been assessed with models that simultaneously consider the effects of land use change and ecosystem processes. Here we take this logical next step by applying four terrestrial biosphere models, each of which has been subjected to a wide range of tests against terrestrial and atmospheric measurements, to simulate the concurrent effects of increases in atmospheric CO_2, interannual climate variability, and cropland establishment and abandonment on terrestrial carbon storage between 1920 and 1992. Our goals are to develop a more consistent quantification of each of these effects, to evaluate the performance of the models in the context of analyses based on extant atmospheric data, and to identify future research efforts that are required to reduce uncertainties among the models.

2. Methods

2.1. Overview

To assess the concurrent effects of increasing atmospheric CO_2 concentration, climate variability, and cropland establishment and abandonment on terrestrial carbon storage between 1920 and 1992, we applied four process-based terrestrial biosphere models (TBMs) to simulate carbon dynamics at 0.5° spatial resolution (latitude by longitude) using a standard simulation protocol in which we ran the models to equilibrium in 1860 and then transiently through 1992 (Figure 1). We performed three simulations with each model. In simulation S1, atmospheric CO_2 concentration alone was varied. In simulation S2, atmospheric CO_2 and climate were varied. In simulation S3, atmospheric CO_2, climate and cropland extent were varied. Our analysis of the simulation results focused on changes in total terrestrial carbon storages and fluxes and their distribution in time and space but did not explicitly consider the transport of carbon from one location to another in the terrestrial biosphere or the exports of carbon to the oceans. Thus decomposition associated with transported carbon, including fluxes released in estuary and coastal marine environments, was implicitly assigned to the grid cell of origin. The difference between S2 and S1 provided estimates of the marginal effect of climate, and the difference between S3 and S2 provided estimates of the marginal effect of cropland establishment and abandonment. We evaluated simulated changes in terrestrial carbon storage associated with biosphere-atmosphere exchanges over two time periods: (1) 1920-1992 and (2) 1980-1989. We also evaluated interannual variability in simulated net terrestrial carbon exchange between 1959 and 1992. Finally, we examined the implications of the simulated carbon exchanges for temporal trends in the seasonal cycle of atmospheric CO_2 between 1961 and 1992.

2.2. Model Descriptions

The four TBMs we applied in this study include the High Resolution Biosphere Model (HRBM) [*Esser et al.,* 1994], the Integrated Biosphere Simulator (IBIS) [*Foley et al.,* 1996;

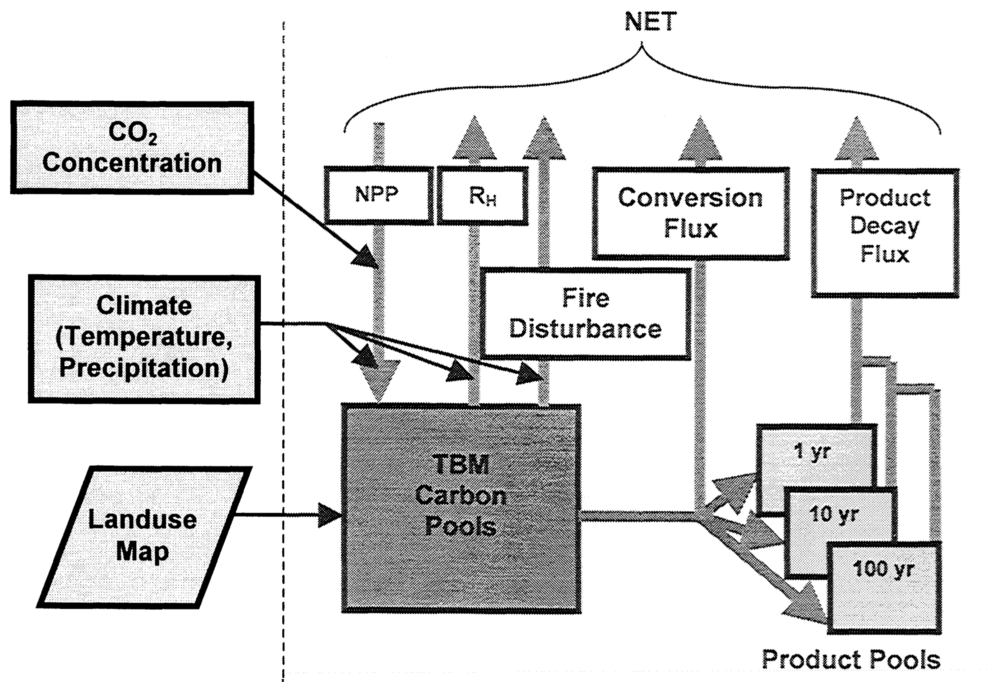

Figure 1. Overview of the simulation protocol implemented by the terrestrial biosphere models (TBMs) in this study to assess the concurrent effects of increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment between 1920 and 1992. Data sets of historical CO_2, climate, and cropland extent were used to drive the models at 0.5° resolution (latitude by longitude). All of the TBMs estimated net primary production (NPP) and heterotrophic respiration (R_H), and some of the TBMs simulated the release of CO_2 as a result of fire disturbance regime. The conversion flux is the simulated release of CO_2 associated with the clearing of land for agriculture, i.e., the burning of slash and fuelwood. Biomass harvested from land as a result of conversion to agriculture or subsequent cultivate were decayed to the atmosphere from three pools with different residence times: a 1-year product pool (decay of agricultural products), a 10-year product pool (paper and paper products), and a 100-year pool (lumber and long-lasting products).

Kucharik et al., 2000), the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ) [*Sitch,* 2000; *Prentice et al.,* 2000], and the Terrestrial Ecosystem Model (TEM) [*Tian et al.,* 1999b]. In this study, three of the models (HRBM, LPJ, and TEM) were applied at 0.5° resolution, while the remaining model (IBIS) was applied at 1° resolution, and the results were interpolated to 0.5° resolution. All four models simulate the exchange of carbon between the atmosphere and the terrestrial biosphere based on spatial and temporal variations in ecosystem structure and physiology but emphasize different aspects of ecosystem dynamics. The simulated changes in ecosystem structure and physiology are related to variations in vegetation type, soil characteristics, atmospheric CO_2 concentration, and climate across the globe. In previous studies, most of these models have estimated net carbon exchange only for potential or natural vegetation. To account for the effect of human disturbance on terrestrial carbon storage in this study, similar algorithms were added to extant code in each model to simulate carbon dynamics resulting from (1) the conversion from natural vegetation to cultivation, (2) production and harvest in cultivated sites, and (3) abandonment of cultivated sites. As only 12% of the terrestrial biosphere has been disturbed by cultivation [*Ramankutty and Foley,* 1998], net carbon exchange from most areas of the globe is estimated using the original algorithms of the models. First we briefly review the characteristics of the extant models used to simulate carbon dynamics in natural ecosystems. Then we describe the modifications to the models that allowed the simulation of net carbon exchange from areas disturbed by cultivation within the context of changing climate and atmospheric CO_2 concentrations.

2.2.1. Natural ecosystems. The models use different approaches to simulate the response of natural terrestrial ecosystems to global change. Each approach is based on simplifying assumptions about the structure of ecosystems and the influence of environmental factors on ecosystem physiology. For example, vegetation distribution is prescribed by input data sets for HRBM and TEM, whereas IBIS and LPJ predict mosaics of plant functional types (e.g., trees and grasses) based on environmental conditions and susceptibility to fire disturbances. To represent the net uptake of atmospheric CO_2 by vegetation, the HRBM uses statistical relationships of NPP with temperature and precipitation, which are then modified as a function of atmospheric CO_2 concentration and soil characteristics. In contrast, IBIS, LPJ, and TEM estimate NPP as the difference between gross primary production (GPP) and plant respiration (R_A) where the influence of environmental factors on these fluxes are calculated. In addition, IBIS, LPJ, and TEM use different formulations to describe the effects of environmental factors on GPP and R_A. Of the four models, TEM is the only model in which dynamic interactions between the carbon and nitrogen cycles of terrestrial ecosystems influence productivity and decomposition rates. In our applications of TEM in this study, we did not consider the effects of anthropogenic nitrogen deposition on NCE. Differences in the representation of ecosystem structure among the models are summarized in Table 1, and differences in ecosystem physiology are summarized in Table 2. Additional details of how the models represent terrestrial ecosystems have been described elsewhere [*Esser et al.*, 1994; *Heimann et al.*, 1998; *Cramer et al.*, 1999; *Kicklighter et al.*, 1999a; *Tian et al.*, 1999b; *Kucharik et al.*, 2000; *Sitch*, 2000; *Prentice et al.*, 2000].

Differences in the representation of terrestrial ecosystems among the models also influence the calculations of net carbon exchange with the atmosphere by the models. In the absence of human disturbance, we calculated NCE for TEM and HRBM as the difference between R_H and NPP:

$$\mathrm{NCE} = R_H - \mathrm{NPP}. \qquad (2)$$

For natural ecosystems, we added an additional term to the right-hand side of (1) for LPJ and IBIS to account for CO_2 emissions from the combustion of biomass due to fire (E_F):

$$\mathrm{NCE} = R_H - \mathrm{NPP} + E_F. \qquad (3)$$

The LPJ model included a climate-driven fire module, which simulates fire occurrence and effects based on vegetation structure, fuel load, and daily litter moisture status [*Sitch*, 2000]. Whereas LPJ simulates a variable fire regime, IBIS assumed constant fire return intervals so that a fixed fraction of each grid cell is disturbed each year.

2.2.2. Cultivated ecosystems. Humans have been replacing the natural vegetation in many areas of the globe for purposes of growing crops. For cultural, economic, and sustainability reasons, many of these areas are later abandoned. Thus three general stages of disturbance that differ with respect to carbon dynamics are associated with cultivated ecosystems. First the conversion from natural vegetation to cultivation generally leads to a net loss of terrestrial carbon to the atmosphere as the biomass of natural vegetation is removed to make resources, such as solar radiation, water, and soil nitrogen, available to crop plants. If economically viable, some of the removed biomass may be incorporated into products for later human consumption, but most of the removed biomass is generally burned. During the second stage, crops are grown, and some biomass is removed from the cultivated ecosystem during harvest. During this stage, soil organic carbon may become depleted because the decomposition of organic matter associated with the original natural vegetation may be greater than the concurrent additions of fresh detritus from crop plants. Finally, the regrowth of secondary vegetation following the abandonment of cultivated sites generally causes these ecosystems to become net sinks of atmospheric CO_2 as carbon is stored in increasing amounts of vegetation biomass and detritus.

In an earlier study, *Houghton et al.* [1983] simulated changes in terrestrial carbon as a result of wood harvest, cultivation and grazing with a bookkeeping model. In their simulations, all carbon storage and rates of carbon loss and gains were prescribed, and the model parameters were stratified by biomes across the globe. The analysis by *Houghton et al.* [1983] also recognized that carbon stored in the products obtained from the ecosystem would be returned to the atmosphere at a variety of rates based on their uses and assigned products into three general decomposition pools: a 1-year pool, a 10-year pool, and a 100-year pool. In this study, we incorporate the approach of *Houghton et al.* [1983] into the algorithms added to all models to track carbon fluxes during the three stages of disturbance and the fate of carbon in products generated from conversion of natural ecosystems to cultivation. Unlike *Houghton et al.* [1983], however, changes in carbon storage are influenced by the relative rates of NPP and R_H and the effects of changing environmental conditions on these fluxes. In addition, the model estimates of the initial carbon storage in vegetation and soils before disturbance are also influenced by spatial and temporal variations in

Table 1. Comparison of the Representation of Ecosystem Structural Dynamics Among Models

	HRBM	IBIS	LPJ	TEM
Plant Functional Types (PFT)	175 vegetation units			
Trees				
evergreen		tropical evergreen, temperate evergreen, cool conifer, boreal conifer	tropical evergreen, temperate broadleaf evergreen, temperate needleleaf evergreen, boreal needleleaf evergreen	tropical evergreen, temperate broadleaved evergreen, temperate conifer, boreal
deciduous		tropical raingreen, temperate summergreen, boreal summergreen	tropical raingreen, temperate summergreen, boreal summergreen	tropical deciduous, temperate deciduous, xeromorphic,
shrubs		n/a	n/a	xeric and mediterranean
grasses, forbs		C_3 photosynthesis, C_4 photosynthesis	C_3 photosynthesis, C_4 photosynthesis	tall, short
Representation of vegetation	four carbon pools (aboveground herbaceous phytomass, belowground herbaceous phyotmass, aboveground woody phytomass, belowground woody phytomass)	three carbon pools (leaves, wood, fine roots)	three carbon pools (leaves, wood, fine roots) per PFT individual; density of individuals	one carbon pool; two nitrogen pools (structural, labile)
Canopy scaling	variable mean stand age	optimum N_{leaf} distribution	optimum N_{leaf} distribution	not explicitly simulated
Phenology				
cold deciduous	dynamic model considering temperature and moisture [*Esser et al.*, 1994]	temperature threshold modified by chilling,	GDD requirement, temperature threshold	evapotranspiration [*Tian et al.*, 1999b]
dry deciduous	dynamic model considering temperature and moisture [*Esser et al.*, 1994]	productivity threshold	soil moisture threshold	evapotranspiration [*Tian et al.*, 1999b]
grass	dynamic model considering temperature and moisture [*Esser et al.*, 1994]	productivity threshold	soil moisture and temperature thresholds	evapotranspiration [*Tian et al.*, 1999b]
Representation of soils	five carbon pools (aboveground herbaceous litter, belowground herbaceous litter, aboveground woody litter, belowground woody litter, soil organic matter)	four litter carbon pools; three soil organic carbon pools; six layers of soil moisture and soil temperature	two litter carbon pools (aboveground and belowground) for each PFT; two soil organic carbon pools (fast, slow) for each PFT	one soil organic carbon pool; one soil organic nitrogen pool; one soil available nitrogen pool; one layer of soil moisture [*Vörösmarty et al.*, 1989; *Tian et al.*, 1999b]
Community dynamics				
competition	not explicitly simulated	homogenous area-based competition for light (two layers), water (six layers)	non-homogenous area-based competition for light (one layer), water (two layers)	not explicitly simulated
establishment	not explicitly simulated	climatically favoured PFTs establish uniformly, as small LAI increment	climatically favoured PFTs establish in proportion to area available, as small individuals	not explicitly simulated
mortality	derived from variable mean stand age [*Esser et al.*, 1994]	deterministic baseline wind throw fire extreme temperatures	deterministic baseline self-thinning carbon balance fire extreme temperatures	not explicitly simulated

Table 2. Comparison of Ecosystem Physiology Among Models

	HRBM	IBIS	LPJ	TEM
Shortest time step	data: 1 month integration: 1 day	1 hour	1 day	1 month determined with an adaptive Runge Kutta Fehlberg integrator [*Cheney and Kincaid*, 1985]
Photosynthesis	NPP based on multiple limiting factors [*Esser et al.*, 1994]	enzyme based [*Farquhar et al.*, 1980; *Collatz et al.*, 1992]	enzyme-based [*Farquhar et al.*, 1980; *Collatz et al.*, 1992]	GPP based on multiple limiting factors [*McGuire et al.*, 1997; *Pan et al.*, 1998]
N uptake by vegetation	not explicitly simulated	not explicitly simulated	not explicitly simulated	dependent on soil available N, air temperature, soil moisture and CO_2 [*McGuire et al.*, 1997; *Pan et al.*, 1998]
Stomatal conductance	not explicitly simulated	Ball and Berry [*Ball et al.*, 1986]	*Haxeltine and Prentice* [1996]	dependent on air temperature, precipitation, solar radiation and soil texture [*Vörösmarty et al.*, 1989; *Pan et al.*, 1996]
Radiation	not explicitly simulated	two stream approximation [*Sellers*, 1985; *Pollard and Thompson*, 1995]	Beer's Law [*Monsi and Saeki*, 1953] applied to vegetation fractions	top of canopy radiation multiplied by relative leaf area [*Tian et al.*, 1999b]
Canopy temperature	not explicitly simulated	canopy energy balance [*Pollard and Thompson*, 1995]	not explicitly simulated	not explicitly simulated
Aerodynamics	not explicitly simulated	log-wind profile+momentum diffusion	not explicitly simulated	not explicitly simulated
Sapwood respiration	not explicitly simulated	diagnose sapwood volume from evaporative demand + LAI	dependent on sapwood mass and C:N ratio and air temperature [*Lloyd and Taylor*, 1994; *Sitch*, 2000]	plant respiration is a function of air temperature and vegetation carbon [*Tian et al.*, 1999b]
Fine root respiration	not explicitly simulated	dependent on root carbon and soil temperature	dependent on root mass and C:N ratio and soil temperature [*Lloyd and Taylor*, 1994; *Sitch*, 2000]	plant respiration is a function of air temperature and vegetation carbon [*Tian et al.*, 1999b]
C allocation	monthly with coefficients for each vegetation type [*Esser et al.*, 1994]	annual with fixed allocation coefficients for leaves, stems, roots	annual allometric relationships for individuals' carbon pools [*Sitch*, 2000]	not explicitly simulated
N allocation	not explicitly simulated	not explicitly simulated	Implicit, dependent upon demand	not explicitly simulated

Table 2. (continued)

	HRBM	IBIS	LPJ	TEM
Litter fall	monthly function of temperature, humidity, soil water and mean stand age [*Esser et al.*, 1994]	annual litter carbon balance	annual litter carbon balance	monthly litterfall C and N is a proportion of vegetation C and N, respectively [*Tian et al.*, 1999b]
Decomposition	dependent on air temperature, humidity and material type [*Esser et al.*, 1994]	dependent on tissue type, soil temperature and soil moisture [*Foley*, 1995]	Dependent on tissue type, soil temperature and soil moisture [*Foley*, 1995]	dependent on soil organic carbon, soil moisture, air temperature [*Tian et al.*, 1999b]
Net N mineralization	not explicitly simulated	not explicitly simulated	not explicitly simulated	dependent on decomposition, C:N ratio of soil organic matter, soil available inorganic nitrogen [*Raich et al.*, 1991]
Evapotranspiration	bucket model [*Esser et al.*, 1994]	based on vapor pressure deficit and stomatal conductance [*Pollard and Thompson*, 1995]	total evapotranspiration [*Monteith*, 1995]	dependent on PET and soil moisture [*Vörösmarty et al.*, 1989]
Water balance	one soil layer bucket model [*Esser et al.*, 1994]	Darcy's Law [*Freeze and Cherry*, 1979] to represent soil moisture surface runoff +drainage snowpack	two soil layers modified bucket model from *Neilson* [1993] surface runoff+drainage snowpack	one soil layer bucket model drainage, snowpack [*Vörösmarty et al.*, 1989]

environmental conditions. For cultivated ecosystems, the estimates of crop NPP are based on the approach of *Esser* [1995], which uses the concept of relative agricultural productivity (RAP). Below we describe how we incorporated the approaches of *Houghton et al.* [1983] and *Esser* [1995] into the simulations of this study.

2.2.3. Conversion from natural vegetation to cultivation. The fate of carbon stored in natural vegetation will be influenced by human decisions during the conversion of land from natural vegetation to agriculture. Economically valuable components of vegetation on a site may be removed from the ecosystem for human consumption if this resource is accessible to markets. Other components of the vegetation may be burned to help clear the land for agriculture, while still other components may simply be left on or in the ground as slash where they will decompose. *Houghton et al.* [1983] calculated the relative proportion of vegetation that is removed for wood or fuels products or left as slash for various biomes across the globe. In this study, each model used the fractions given by *Houghton et al.* [1983, Table 1] if they were not already explicitly modeled. For example, LPJ explicitly estimates belowground vegetation carbon (roots), and therefore Houghton's fraction of vegetation carbon left dead in soils was ignored. In this case, the estimate of aboveground vegetation carbon was assigned to the product decay pools using the given ratios (e.g., 40:27 in the case of tropical forest conversion for the ratio of the loss of aboveground carbon to emissions on conversion versus loss to products; see Table 3). Therefore, while we relied on the mechanisms represented in the models, the retention of some formulations from *Houghton et al.* [1983] simplified our analysis and allowed us to compare the results of our mechanistic approach with the results of the bookkeeping approach while controlling for some of the assumptions in each approach. Each model was free to assign the vegetation carbon left dead in soils to particular soil pools and to decide upon the seasonal timing of inputs into the soil and product pools. If a grid cell was assumed to be a mixture of vegetation types, the appropriate conversion rates were applied to each of the vegetation types and weighted by the areal proportion of the vegetation type in the grid cell. During conversion, aboveground carbon could be either immediately consumed when fire is used as the conversion tool or used as fuelwood, paper and paper products, or for lumber and long-lasting products [*Houghton et al.*, 1983]. We refer to the carbon oxidized within 1 year of conversion as the conversion flux (see Figure 1). The conversion flux includes biomass consumed by fire during conversion and fuelwood harvest. The implementation of the seasonal timing of the conversion flux was left for each model to decide.

2.2.4. Production and harvest in cultivated sites. Because this study represents a first attempt to combine the dominant effects of land use and land-cover change on historical terrestrial carbon storage with the mechanistic responses of terrestrial ecosystems to atmospheric CO_2 and climate, we decided to adopt the simple RAP approach of *Esser* [1995] instead of explicitly parameterizing croplands. By standardizing on this approach, we were able to avoid confounding the interpretation of the comparison among models that might be associated with fundamental design changes in the extant models, which would be necessary when introducing the various crop types as new biomes or plant functional types. To calculate the NPP of

Table 3. The Fate of Carbon for Different Terrestrial Ecosystems Upon Conversion to Agriculture Implemented by the Models in This Study for Simulations That Considered the Effects of Cropland Establishment and Abandonment

Ecosystem	Left Dead in Soils (Root Biomass), %	1st Year Conversion Loss (Conversion Flux-Fuel Wood, Biomass burning, etc.), %	10-Year Product Pool, PROD10 (Wood Pulp, Paper, etc.), %	100-Year Product Pool, PROD100 (Wood Furniture, etc.), %
Temperate/boreal forest	33	40	20	7
Tropical forest	33	40	27	0
Grasslands/tundra	50	50	0	0
Shrublands, woodlands, savannas	50	40	10	0

Based on *Houghton et al.* [1983].

agricultural lands with the RAP approach, we multiplied the NPP of the natural vegetation by the RAP defined for each grid cell:

$$NPP_{agric} = RAP \otimes NPP_{nat}, \quad (4)$$

where NPP_{agric} and NPP_{nat} are the annual net primary production under agricultural and natural vegetation cover, respectively. We defined NPP_{nat} for a particular grid cell as the annual NPP simulated for the grid cell in simulation experiment S2. The estimate of annual agricultural NPP was divided into aboveground and belowground biomass, i.e., harvest versus residue, using the ratio 40:60. The harvested NPP was placed in the agricultural products pool, which is a product pool that decays to the atmosphere in one year (see Figure 1). The belowground biomass entered the soil. *Malmström et al.* [1997] reported estimated yields that ranged from ~20% of annual NPP at the low end to ~50% of annual NPP at the high end (see Malmström et al. [1997, Table 2]). Thus the harvest of 40% annual NPP in this study may represent a high estimate for carbon allocated to the agricultural products pool.

2.2.5. Abandonment of cultivated sites. In the second half of this century, large areas in temperate North America and Europe previously cultivated have been abandoned, and natural vegetation has been allowed to regrow. Each model grew back vegetation biomass from the extant state of the grid cell at the time of abandonment. Unlike *Houghton et al.* [1983], who prescribed the time required for the ecosystem recovery to disturbance, environmental factors influence the simulated recovery of ecosystems from human disturbance in the simulations of this study.

2.2.6. Fate of land use products. Land use products were divided into three pools, which represent the fate of the aboveground biomass at the time of conversion and the subsequent agricultural yield. Paper and paper products decayed over 10 years, and lumber and long-lasting products decayed over 100 years. As mentioned earlier, agricultural products were assumed to be consumed within 1 year. The sum of the fluxes released to the atmosphere from the three product pools are collectively referred to as the product flux (Figure 1). Annual releases from the three pools were calculated as a linear decay of the initial carbon inputs into these pools over 1, 10, and 100 years, respectively. For example, the annual release from the 10-year product pool represents 10% of the initial carbon that has entered the pool during the previous 10 years. Therefore 10 years after conversion to agriculture all of the initial carbon entering the pool will have been released to the atmosphere. For this analysis, we assumed that releases were associated with the grid cell of origin. Similar to the conversion flux, the seasonal timing of the CO_2 release from the three pools was left for each model to decide. Thus we calculated annual NCE for a particular grid cell differently for a grid cell that has been disturbed by cultivation than for one covered with undisturbed vegetation. For HRBM and TEM, we calculated the net carbon exchange as

$$NCE = R_H - NPP + E_C + E_P, \quad (5)$$

where E_C is the carbon emissions during the conversion of natural ecosystems to cultivation and E_P is the sum of carbon emissions from the decomposition of products. For IBIS and LPJ, our estimates of net carbon exchange also consider the loss of terrestrial carbon due to fires not associated with conversion to agriculture:

$$NCE = R_H - NPP + E_F + E_C + E_P \quad (6)$$

2.3. Data Sets

2.3.1. Historical atmospheric CO_2. We developed a data set of historical atmospheric CO_2 that extends from 1860 through 1992. For the time period 1860-1958, which was before direct observations are available, we derived the time series of the historical atmospheric CO_2 mixing ratio using a spline fit to the ice-core record of *Etheridge et al.* [1996]. For the time period from 1959 to 1995, we averaged the observations from Mauna Loa and South Pole [*Keeling et al.,* 1995]. Since the ice-core measurements of *Etheridge et al.* [1996] extended until the early 1970s, we merged the records in a smooth fashion during a 5-year transition zone between 1958 and 1962 using a linear interpolation between the two records.

2.3.2. Temperature and precipitation. To provide climate inputs for the simulations in this study, we developed global monthly fields of surface temperature and precipitation for the time period 1900-1992 gridded to 0.5° resolution, which in the simulation experiments S2 and S3 were superimposed as anomalies on the standard climatologies employed by the different models. We derived the temperature fields from the observed temperature anomaly fields compiled on a 5° x 5°

global grid by *Jones* [1994] from global weather station data. For grid-squares with missing observations, we interpolated from adjacent grid-squares. For driving the models in the simulations of this study, we superimposed the monthly temperature anomalies using bilinear interpolation on version 2.1 of the 0.5° x 0.5° CLIMATE database [*Leemans and Cramer,* 1991; *W. Cramer,* unpublished data, 1994] employed by the models. We derived the precipitation fields from the monthly precipitation observations compiled on a global 3.75° x 2.50° grid by *Hulme* [1992, 1994]. For grid-squares with missing observations, we used interpolated values. Subsequently, we determined precipitation factors relative to a monthly climatology over the time period from 1950 to 1980 and bilinearly interpolated to 0.5° resolution. For driving the models in the simulations of this study, we multiplied these time varying precipitation factors with the climatological precipitation fields from the CLIMATE database. For the initialization of the models, we extended these data sets back over the time period from 1860 to 1899. We derived the temperature fields between 1860 and 1899 from the observations of *Jones* [1994] as described above. Since no global gridded precipitation observations were available prior to 1900, we generated surrogate time varying precipitation fields by randomly selecting individual years between 1900 and 1929. Because monthly precipitation is strongly correlated with monthly temperature in some parts of the world, we preserved this relationship in grid cells that exhibited this behavior in the precipitation fields prior to 1900.

2.3.3. Historical land use and relative agricultural productivity (RAP). We derived the historical croplands data set used in this study (see Figure 2) from the historical fractional croplands data set of *Ramankutty and Foley* [1998, 1999]. The fractional croplands data set, which describes the fraction of a 0.5° grid cell in croplands between 1700 and 1992, was developed from a simple algorithm to synthesize a land-cover classification data set derived from satellite observations [*Loveland and Belward,* 1997] with contemporary and historical cropland inventory data collected from various census organizations. Because the fractional croplands data set does not describe cohorts of unique land use change trajectories within each 0.5° grid cell, we developed a boolean croplands data set between 1860 and 1992 to describe unique land use change trajectories at 0.5° resolution. In the boolean croplands data set, each 0.5° grid cell is completely represented as either agricultural or natural ecosystems. We developed the boolean croplands data set by employing an algorithm that preserves total cropland areas at large spatial scales (see Figure 3). Specifically, boolean values for each of the 100 0.5° grid cells contained within every 5° grid cell were chosen such that the total cropland area calculated over the 5° grid cell from the boolean 0.5° data matched the total calculated each year from the continuous data set. The 0.5° grid cells with higher fractional cropland areas among the 100 0.5° grid cells were assigned to agricultural ecosystems before grid cells containing less fractional cropland area. Furthermore, to prevent cases where grid cells shifted back and forth interannually between croplands and no croplands, we applied a 9-year running filter to the data set. The choice of the 9-year running filter corresponded to the nominal decadal-scale resolution of the census statistics used by *Ramankutty and Foley*

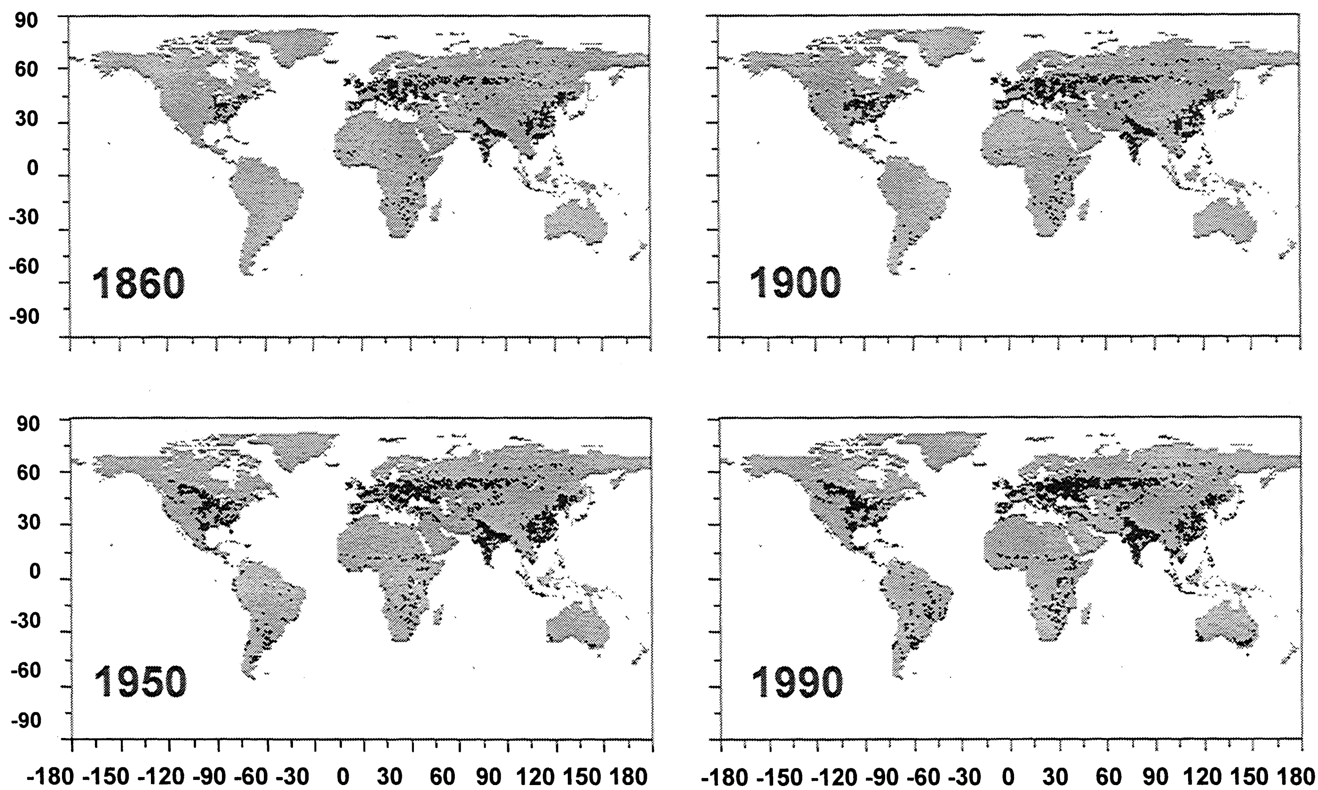

Figure 2. Snapshots of the extent of global croplands in 1860, 1900, 1950, and 1990 from the boolean 0.5° historical croplands data set used to drive the models in this study.

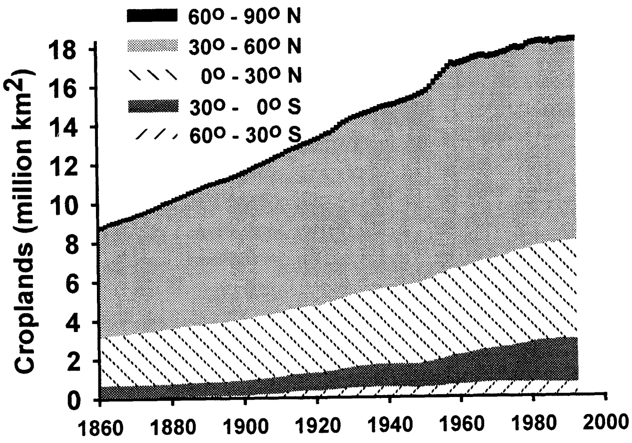

Figure 3. The area occupied by croplands for 30°-latitude bands between 1860 and 1992 from the boolean 0.5° historical croplands data set used to drive the models in this study.

[1999] to develop the parent croplands data set. We used the boolean croplands data set to specify the temporal and spatial features of the RAP data set, which we derived from country-specific data as described by *Esser* [1995] to define the agricultural productivity relative to the productivity of the natural vegetation.

2.3.4. Other data sets. Because the vegetation and soil data sets used by different models are often linked explicitly to vegetation- and soil-specific parameters in the models, we decided to not standardize these data sets, which represent differences in vegetation and soil classifications. In this study, TEM used the potential natural vegetation map described by *Melillo et al.* [1993], HRBM used the vegetation distribution described by application of the BIOME model [*Prentice et al.*, 1992], and IBIS and LPJ used the natural vegetation cover that the models simulated for each grid cell. Although the description of soil type and texture are different among models, the soils data are based on the *Food and Agriculture Organization/United Nations Educational, Scientific and Cultural Organization (FAO/UNESCO)* [1974] soil map of the world (TEM and HRBM), the *Zobler* [1986] soil classes (IBIS), or a combination of the two (LPJ). Annual radiation records or its proxies, for example, cloudiness or sunshine, were not available in sufficient density to develop a historical global radiation data set. Therefore the models either used the mean monthly percent sunshine hours directly from *Cramer and Leemans* database (*W. Cramer*, personal communication, 1994), which represents means over the years from 1931 to 1960 or derived the incoming solar radiation using a common methodology. If necessary, the monthly values were interpolated to daily and hourly time steps using simple interpolation schemes and periodic functions, depending on the specific requirements of the individual model.

2.4. Simulation Protocol

For all simulations, we initialized the models with the 1860 atmospheric CO_2 concentration of 286.6 ppmv. The HRBM, IBIS, and TEM models, which were initialized with a baseline mean climate that we derived from the historical climate data we developed for the period from 1860 to 1899, were run until equilibrium was reached with respect to the carbon pools of each model. In addition, the nitrogen pools of TEM and vegetation cover of IBIS were in equilibrium at the end of initialization. Because the fire module of LPJ requires climate data with interannual variability, LPJ was initialized by repeating the 1860-1899 climate sequence until a dynamic equilibrium was achieved for the 40-year period. For simulation experiment S3, each model used agricultural NPP to simulate equilibrium soil carbon at initialization for the grid cells defined as cropland in 1860. Therefore, compared to simulation experiments S1 and S2, the total terrestrial carbon storage at the completion of initialization was always lower in simulation experiment S3 because vegetation and soil carbon of croplands were generally less than carbon storage in the natural vegetation. At the completion of initialization, the 10-year and 100-year product pools were empty, and none of the models simulated a conversion flux or product fluxes for the final initialization year. We used the January climate of 1860 and the December values of the state variables from the final initialization year to start the transient phase of each simulation, which extended from 1860 through 1992. In addition to the use of the historical CO_2 data set for the transient phase of simulation S1, HRBM, IBIS, and TEM used the initialization baseline mean climate while LPJ used the 40-year initialization climate with interannual variability. For the LPJ S1 simulation, we fit cubic splines to the annual NPP, R_H, and E_F of each 15° latitude band to remove the effects of interannual climate variability for purposes of comparing the S1 simulations among all the models. This processing procedure did not affect the long-term changes in carbon storage simulated by LPJ in simulation experiment S1. For simulation experiments S2 and S3, the transient phase of each model simulation was driven by historical CO_2 and historical climate based on a complete set of observed temperature fields and reconstructed precipitation fields for the time period from 1860 to 1899 and based on observations from 1900 to 1992. We also used the boolean croplands data set and the RAP data set to simulate the effects of cropland establishment and abandonment between 1860 and 1992 in simulation experiment S3.

2.5. Comparisons With Analyses Based on Atmospheric Data

Because the climate data we used in this study do not represent real climate until 1900 and the density of precipitation measurements early in this century is rather poor in comparison with the more recent decades, we do not begin our analysis until 1920. We evaluated the modeled biosphere-atmosphere exchanges for two time periods (1920-1992 and 1980-1989) in the context of analyses based on atmospheric data. For the period between 1920 and 1992, we compared simulated exchanges with observationally based analyses on long-term responses, decadal responses, interannual variability, and trends in features of the seasonal cycle. For the 1980s, we evaluated global and latitudinal patterns in carbon exchange simulated by the models in the context of IPCC analyses for the period [*Schimel et al.*, 1996].

To evaluate the long-term responses of carbon exchange, we compared model simulations to results of a "double deconvolution" reconstruction of decadal-scale variations in terrestrial carbon storage [*Joos et al.*, 1999]. In the double deconvolution, the two budget equations for atmospheric CO_2 and ^{13}C are solved for the global unknown fluxes between the atmosphere and the terrestrial biosphere and between the atmosphere and the oceans. The CO_2 budget yields the total flux into the ocean plus biosphere to equal the change in the atmospheric carbon inventory [*Etheridge et al.,* 1996] minus fossil carbon emissions. The ^{13}C budget is used to partition between the oceanic and terrestrial sink fluxes that carry different isotopic signatures. Changes in the atmospheric ^{13}C are obtained from ice core (1000-1980 A.D.) and direct atmospheric measurements [*Francey et al.,* 1999]. Uncertainties in the reconstructed fluxes, which are associated with uncertainies in the ^{13}C and CO_2 data, fossil emission data, isotopic fractionation, and ^{13}C isotopic disequilibrium fluxes associated with gross carbon exchange fluxes are estimated to be +/- 0.3 Pg C yr^{-1} (1 standard deviation) prior to 1950 and then to increase linearly to +/- 0.8 Pg C yr^{-1} in 1990 [*Joos and Bruno,* 1998].

In addition to comparison with the long-term deconvolution analysis, we compared the responses of net terrestrial carbon exchange at the end of the transient phase with independent estimates for the 1980s and 1990s based on observed global atmospheric CO_2 and O_2 budgets. These measurements provide a purely observational estimate of the carbon uptake by the terrestrial biosphere and oceans [*Keeling and Shertz,* 1992; *R. F. Keeling et al.,* 1996; *Bender et al.,* 1996]. The updated budgets employed here are based on updated O_2 measurements from the 1980s [*Langenfelds et al.,* 1999] and from the 1990s [*Battle et al.,* 2000]. The associated error estimates reflect uncertainties in the estimation of the decadal trends in the global atmospheric O_2 concentration, in the magnitude of fossil fuel emissions, and in the average stoichiometric relations between CO_2 and O_2 associated with fossil fuel burning, biospheric photosynthesis, and oxidation of organic matter [*Keeling et al.,* 1993].

For the time period of direct atmospheric CO_2 observations (1959-1992), we assessed the modeled interannual variability by comparison with results of a single deconvolution analysis of the atmospheric CO_2 budget. In this analysis the globally averaged, seasonally corrected atmospheric growth rate of CO_2 estimated from the Mauna Loa and the South Pole records [*Keeling et al.,* 1995] is assumed to reflect the global, time-varying net carbon flux to the atmosphere, dN_a/dt. This flux is composed of (1) the emissions from fossil fuel burning and cement production derived from statistics of energy production [*Marland et al.,* 1999], Q_{foss}, (2) ocean uptake computed by a three-dimensional ocean carbon cycle model [*Maier-Reimer,* 1993], S_{ocean}, and (3) a residual, attributed to a net terrestrial carbon flux, Q_{terr}:

$$dN_a/dt = Q_{foss} - S_{ocean} + Q_{terr}.$$

Clearly, Q_{terr} constructed this way also includes climate driven carbon exchanges of the atmosphere with the ocean that are not simulated by the ocean model. In comparing Q_{terr} with the results of the TBMs, we implicitly assume that the interannual, climate driven oceanic variability to this flux is small compared with the terrestrial contributions [*Lee et al.,* 1998; *Feely et al.,* 1999]. There exists, however, a conflicting analysis based on atmospheric $^{13}C/^{12}C$ observations [*Keeling et al.,* 1995].

Besides the long-term increases and interannual variability in atmospheric CO_2 that are observable from the CO_2 record at Mauna Loa, the record also exhibits a prominent increase and interannual variation of the amplitude of the seasonal cycle [*C. D. Keeling et al.,* 1996]. In addition to small contributions from fossil fuel [*Heimann et al.,* 1986], most of this signal is caused by variations in the timing and magnitude of seasonal carbon exchanges between the atmosphere and terrestrial processes in the temperate Northern Hemisphere. The remote Mauna Loa station has been shown to reflect a close average of the portion of the terrestrial biosphere in the Northern Hemisphere [*Kaminski et al.,* 1996]. This signal provides a unique additional, independent means to evaluate the performance of TBMs. In this study, we compared the relative change in the seasonal cycle associated with simulations of the TBMs with the observations of *C. D. Keeling et al.* [1996] of the relative increase of the seasonal cycle since the baseline period of 1960-1964. The relative change in the seasonal cycle for each TBM was determined by accumulating the simulated monthly fluxes north of 30°N in a single atmospheric box model. The amplitude of the seasonal concentration signal in this box was evaluated for each simulated year and expressed as a scaling factor relative to the 5-year average of the seasonal cycle of years from 1960 to 1964. These annual scaling factors were then subsequently compared to the scaling factors determined in a similar way from the observations [*C. D. Keeling et al.,* 1996].

3. Results

3.1. Long-Term Changes in Carbon Storage (1920-1992)

Across the time period from 1920 to 1992, simulations by HRBM and IBIS indicate that terrestrial ecosystems have stored small amounts of carbon, largely because storage associated with the effects of CO_2 fertilization is greater than net releases associated with land use (Figure 4). In contrast, the simulations by LPJ and TEM indicate that terrestrial ecosystems have lost small amounts of carbon across the period because net releases associated with land use are greater than storage associated with CO_2 fertilization. The models agree that the effects of climate are small in comparison with the effects of CO_2 fertilization, cropland establishment, and cropland abandonment.

Although the models agree that the effects of climate on carbon storage are small in comparison with CO_2 and land use, the effects of climate differ among the simulations by the TBMs (Figure 4). In HRBM, climate variability promoted carbon storage in terrestrial ecosystems while in IBIS and LPJ, climate promoted carbon release. In TEM, climate variability promoted carbon release until the 1960s when it began to promote carbon storage. For the marginal effects of cropland establishment and abandonment between 1920 and 1992, the magnitude is not strictly associated with the magnitude of carbon storage simulated by the models. Thus the processes represented in the models are responsible, in part, for the variability in the simulated effects of cropland establishment and abandonment among the models.

The 10-year running mean of the annual net carbon exchange simulated by the TBMs ranges from approximately neutral to releases until around 1970 and indicates substantial storage after 1970 (Figure 5), which suggests that the terrestrial biosphere switched to net carbon uptake during the 1960s. The storage in the 1960s appears to be associated with both the fertilization effects of atmospheric CO_2, which started to increase rapidly during this period, and CO_2 releases associated with the global effects of land use, which peaked in the late 1950s and decreased throughout the 1960s in the simulations by all the models (Figure 6) because of a deceleration in the expansion of croplands (Figure 3). Because the models agree that the net carbon exchange of

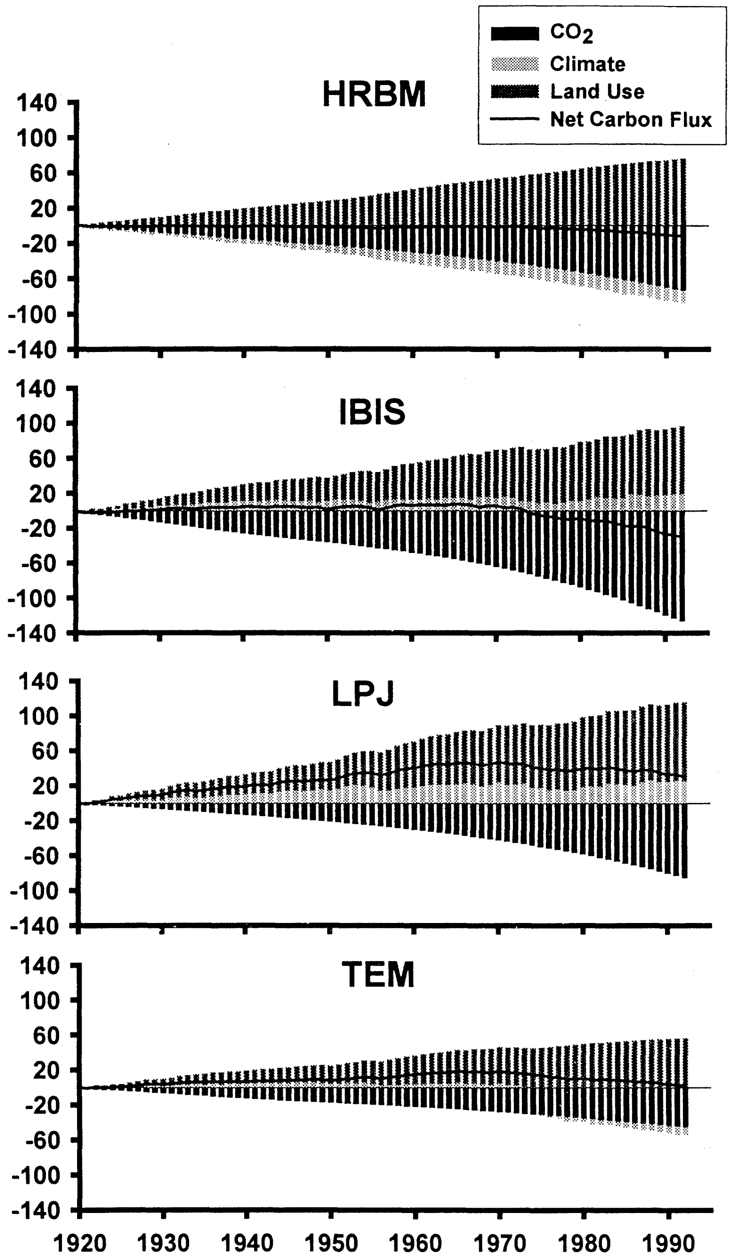

Figure 4. The cumulative change in net carbon storage in 1920 estimated by the terrestrial biosphere models in simulations that considered the effects of increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment. The cumulative change in net carbon storage associated with increasing atmospheric CO_2 is estimated from a simulation that considered only increasing CO_2. The cumulative change in net carbon storage associated with climate variability was estimated by subtracting the cumulative change of a simulation that considered only increasing atmospheric CO_2 from that of a simulation that considered both increasing atmospheric CO_2 and climate variability. The cumulative change in net carbon storage associated with cropland establishment and abandonment was estimated by subtracting the cumulative change of a simulation that considered increasing atmospheric CO_2 and climate from that of a simulation that considered increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment. Positive values indicate net releases to the atmosphere and negative values indicate net storage in terrestrial ecosystems.

terrestrial ecosystems has been characterized by carbon storage since about 1960, we evaluated the effects of CO_2, climate, and land use before and after 1958 (Table 4), which is the year that continuous atmospheric measurements began at Mauna Loa. Before 1958, simulations by three of the models (IBIS, LPJ, and TEM) indicate net release of carbon to the atmosphere because releases associated with cropland establishment and climate are greater than storage associated with the effects of rising atmospheric CO_2 (Table 4). In contrast to the other TBMs, HRBM simulates a small amount of net carbon storage between

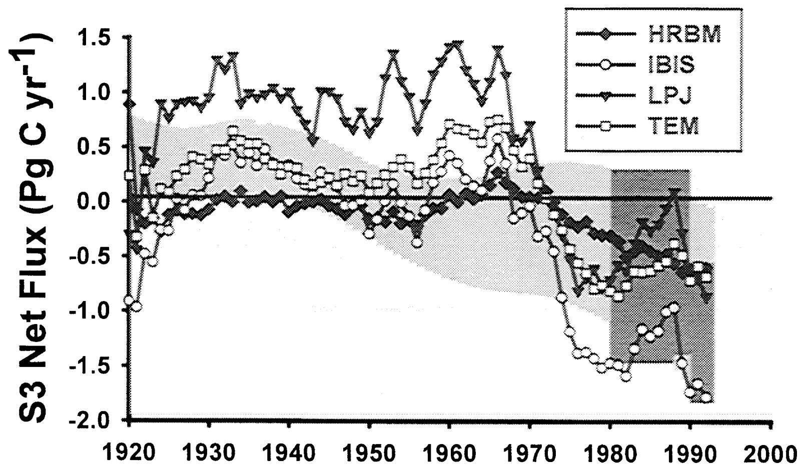

Figure 5. The 10-year running means of the global net carbon exchange with the atmosphere estimated by each of four terrestrial biosphere models (HRBM, IBIS, LPJ, and TEM) between 1920 and 1992 in simulations that considered the effects of rising atmospheric CO_2, climate variability, and cropland establishment and abandonment. Running means were calculated starting in 1860, which was the year that the models were initialized. The light shaded region represents the uncertainty (+/- one standard deviation) of net carbon exchanged estimated by a double deconvolution analysis (see section 2). The dark shaded regions represent the uncertainty (+/- one standard deviation) estimated by analyses of CO_2 and O_2 budgets in the 1980s and 1990s (see section 2). Positive values indicate net releases to the atmosphere and negative values indicate net storage in terrestrial ecosystems.

1920 and 1957 because the effects of both CO_2 fertilization and climate are slightly greater than the effects of land use.

Between 1958 and 1992, the simulations by all TBMs indicate net carbon storage in the terrestrial biosphere because the effects of CO_2 fertilization dominate releases associated with other factors (Table 4). Among the simulations by the TBMs, the range of storage associated with CO_2 fertilization (25.0-82.6 Pg C) is greater than the range of storage/release associated with climate (10.9 Pg C storage to 11.3 Pg C release) and the range of release associated with cropland establishment/abandonment (27.0-43.8 Pg C). The higher storage simulated by IBIS occurs because the effect of CO_2 fertilization is about twice the release associated

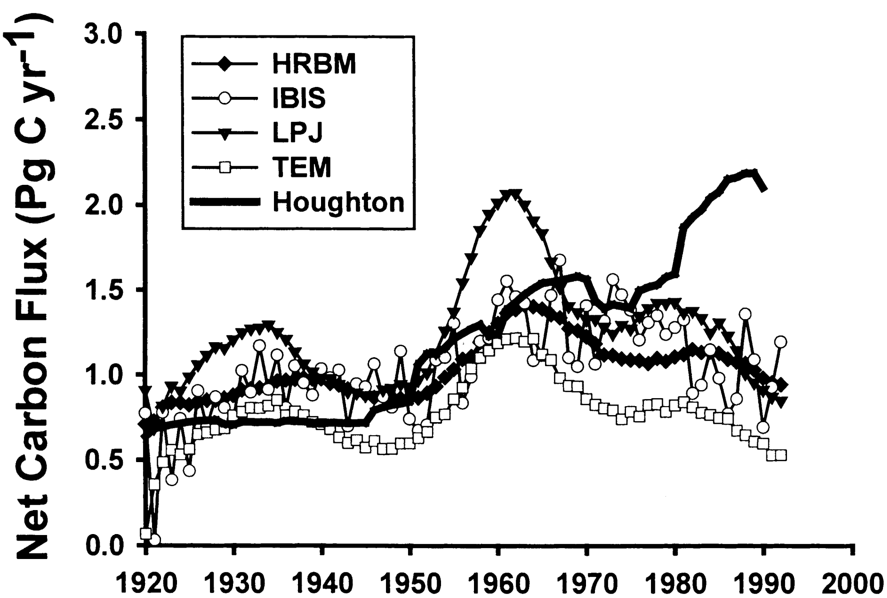

Figure 6. The 10-year running means of global annual net release of CO_2 to the atmosphere associated with cropland establishment and abandonment between 1920 and 1992 estimated by the simulations of four terrestrial biosphere models (HRBM, IBIS, LPJ, and TEM) compared with the release estimated by the bookkeeping model of *Houghton* [1999], which considered the conversion of forests to pasture in addition to cropland establishment and abandonment. The annual release in net carbon storage associated with cropland establishment and abandonment was estimated by subtracting the cumulative change of a simulation that considered increasing atmospheric CO_2 and climate from that of a simulation that considered both increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment.

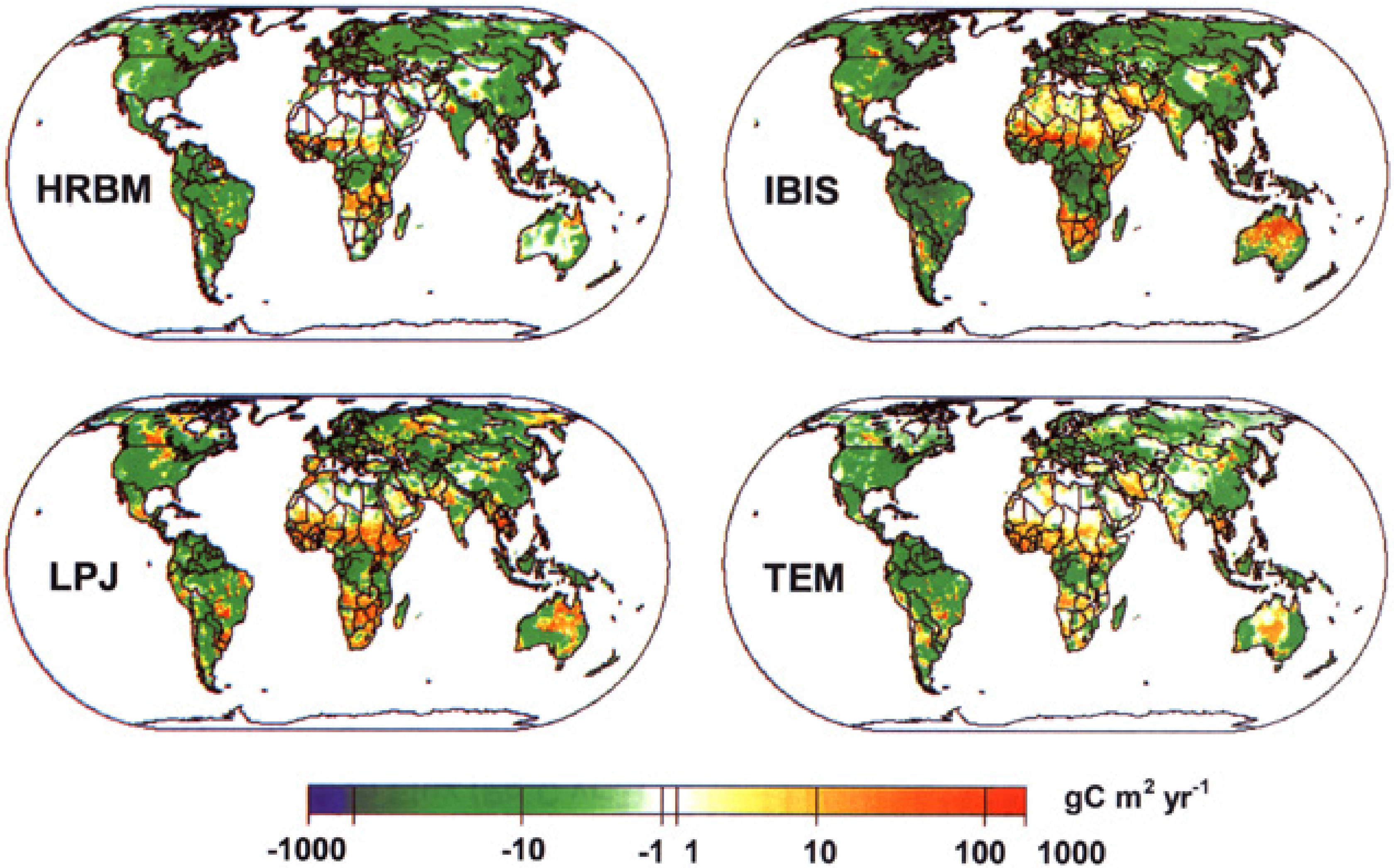

Plate 1. The spatial distribution of the mean annual net carbon exchange with the atmosphere from 1980 through 1989 estimated by each of four terrestrial biosphere models in a simulation that considered the effects of increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment. Positive values indicate net releases to the atmosphere and negative values indicate net storage in terrestrial ecosystems.

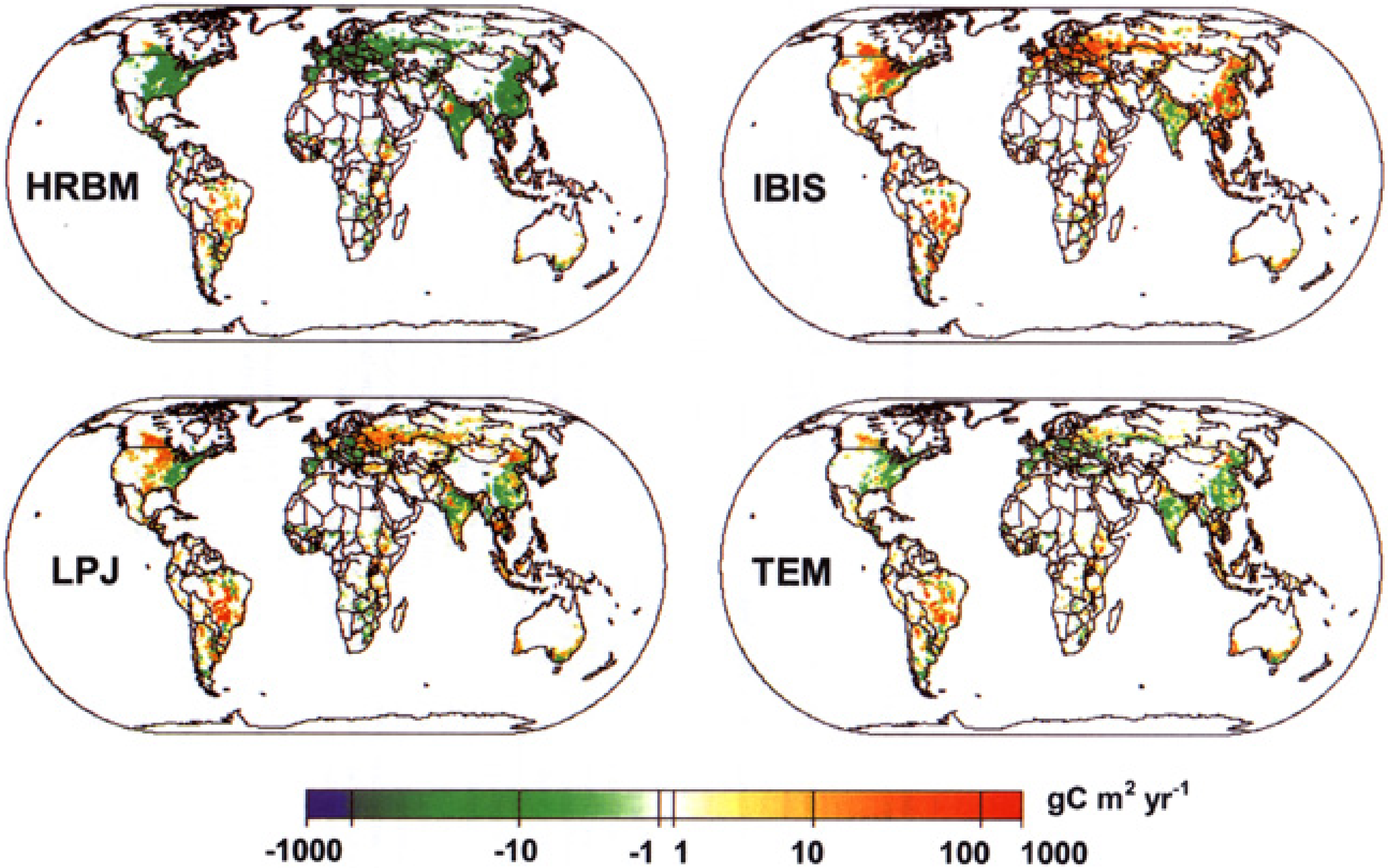

Plate 2. The spatial distribution of the mean annual net carbon exchange with the atmosphere from 1980 through 1989 associated with cropland establishment and abandonment as estimated by each of four terrestrial biosphere models. The change in net carbon storage associated with cropland establishment and abandonment was estimated by subtracting the cumulative change of a simulation that considered increasing atmospheric CO_2 and climate from that of a simulation that considered both increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment. Positive values indicate net releases to the atmosphere and negative values indicate net storage in terrestrial ecosystems.

Table 4. Partitioning of Cumulative Changes in Global Terrestrial Carbon Storage Between 1920 and 1957 and Between 1958 and 1992 Among Effects Attributable to Changes in Increasing Atmospheric CO_2, Climate Variability, and Cropland Establishment and Abandonment

Timeframe	Effect	HRBM	IBIS	LPJ	TEM
1920 - 1957	CO_2	-27.5	-43.6	-27.0	-19.9
	climate	-11.8	9.6	14.2	2.2
	land use	36.6	36.8	47.0	29.2
	total	-2.7	2.8	34.2	11.5
1958 - 1992	CO_2	-45.9	-82.6	-57.3	-25.0
	climate	-2.2	11.3	9.6	-10.9
	land Use	39.5	38.1	43.8	27.0
	total	-8.6	-33.2	-3.9	-8.9

Positive values indicate net releases to the atmosphere, and negative values indicate net storage in terrestrial ecosystems. Storage values are given in Pg C.

with land use, whereas the magnitudes of these effects are similar for the other models.

3.2. Changes in Carbon Storage Between 1980-1989

During the 1980s, the simulations by the TBMs indicate that the net exchange of CO_2 with the atmosphere resulted in a net carbon storage in terrestrial ecosystems of between 0.3 and 1.5 Pg C yr^{-1} (Table 5). At the global scale, all models indicate that the effects of CO_2 fertilization are stronger than releases associated with land use. The simulation by IBIS indicates that the effect of CO_2 fertilization is slightly stronger north of the tropics than in the tropics, while simulations by the other models indicate that the CO_2 effect is slightly stronger in the tropics than north of the tropics. Simulations by all models indicate that cropland establishment/abandonment has caused the release of carbon to the atmosphere, primarily associated with land use in the tropics. The higher land use estimate of storage by HRBM north of the tropics is primarily associated with a lower flux from the decomposition of agricultural, paper, and wood products (0.4 Pg C) in comparison with the other three models (1.1-1.8 Pg C). The models disagree about the sign and the magnitude of the effects of climate on global carbon storage. The simulations of both HRBM and TEM indicate that the effects of climate tend to promote carbon storage and that the effects are small in comparison with the effects of CO_2 and land use. In contrast, the simulations of both IBIS and LPJ indicate that climate promotes carbon release and that the effects are similar in magnitude to the effects of land use.

Three of the four models indicated that the tropics were approximately neutral (-0.2-0.2 Pg C yr^{-1}) during the 1980s (Table 5), and there is substantial spatial variation simulated by all the models throughout the tropics (Plate 1). In general the models simulate net sink activity in the tropical Western Hemisphere and Asia (Plate 1) because the effects of CO_2 fertilization exceed releases associated with cropland establishment, which are most pronounced in tropical South America (Plate 2). The models also indicate substantial source activity in some parts of tropical Africa (Plate 1), which is largely associated with the effects of climate as cropland establishment does not appear to be responsible for substantial releases from the region (Plate 2). The simulations by all the models indicate that ecosystems north of the tropics acted as a sink for atmospheric CO_2 during the 1980s, with uptake by terrestrial ecosystems strongest in the north central United States, northern Europe, and eastern China (Plate 1). The simulations by TEM and LPJ indicate that the land use component is approximately neutral north of the tropics (Plate 2) because the effects of carbon storage associated with forest regrowth are approximately balanced by releases associated with the decomposition of agricultural, paper, and wood products north of the tropics. In contrast, the simulation by HRBM indicates that the land use component caused net carbon storage in the region (Plate 1) because the effects of forest regrowth are greater than the releases from the decay of products, while the simulation by IBIS indicates a net release for the land use component (Plate 2) because the releases from products are apparently greater than the effects of forest regrowth.

3.3. Interannual Variability in Net Terrestrial Carbon Exchange (1959-1992)

Although the simulations by the TBMs generally agree on the timing of net release and net storage of CO_2 by terrestrial ecosystems between 1959 and 1992, there are substantial differences in the magnitude of simulated interannual variability among the simulations (Figure 7). For HRBM, the magnitudes of interannual variability in NPP and R_H are approximately equal, whereas in the other three models, interannual variability in carbon storage is primarily associated with interannual variability in NPP. The substantial releases simulated by LPJ in certain years (e.g., 1983 and 1987), which tend to be larger than releases

Table 5. Partitioning of Mean Annual Changes in Terrestrial Carbon Storage Between 1980 and 1989 Among Effects Attributable to Changes in Increasing Atmospheric CO_2, Climate Variability, and Cropland Establishment and Abandonment for Global Ecosystems, for Ecosystems North of 30°N, for Ecosystems in the Tropics Between 30°N and 30°S, and for Ecosystems South of 30°S

Region	Effect	HRBM	IBIS	LPJ	TEM
Global	CO_2	-1.6	-3.1	-2.1	-0.9
	climate	0.0	0.8	0.9	-0.2
	land use	1.0	0.8	0.9	0.6
	total	-0.6	-1.5	-0.3	-0.5
North	CO_2	-0.7	-1.6	-0.9	-0.2
	climate	-0.2	0.0	0.4	-0.1
	land use	-0.4	0.3	0.1	0.0
	total	-1.3	-1.3	-0.4	-0.3
Tropics	CO_2	-0.9	-1.4	-1.1	-0.6
	climate	0.2	0.7	0.5	-0.1
	land use	1.2	0.5	0.8	0.6
	total	0.5	-0.2	0.2	-0.1
South	CO_2	-0.1	-0.1	0.0	0.0
	climate	0.0	0.0	0.0	0.0
	land use	0.3	0.1	0.0	0.0
	total	0.2	0.0	0.0	0.0

Positive values indicate net releases to the atmosphere, and negative values iindicate net storage in terrestrial ecosystems. Storage values are given in Pg C yr^{-1}.

simulated by the other TBMs, are associated primarily with lower NPP and secondarily with higher emissions in tropical fires in comparison to other years. Both IBIS and LPJ tend to simulate large amounts of storage in certain years (e.g., 1974, 1984, and 1989) largely because of higher NPP in those years. Interannual variability in both the HRBM and TEM simulations is also associated with lower NPP in 1983 and 1987 and with higher NPP in 1974, 1984, and 1989, but the range in variability of NPP is much less than in the LPJ and IBIS simulations.

3.4. Simulated Trends in the Seasonal Cycle at Mauna Loa (1961-1992)

We simulated the seasonal cycle at Mauna Loa by redistributing the monthly net fluxes of the S1, S2, and S3 simulations with an atmospheric transport model and calculated the relative change in the amplitude of the seasonal cycle across the time period (Figure 8 and Table 6). The analysis for the S1 simulations indicates that CO_2 fertilization in all models causes the amplitude of the seasonal cycle to increase between 1961 and 1992. The strength of this pattern among the models is similar to the magnitude of the CO_2 fertilization effect in the models between 1958 and 1992 north of the tropics (see Table 4). Compared to the results for the S1 simulations, the addition of climate variability in the S2 simulations strengthens the trend for LPJ, weakens the trend for TEM, and has little effect on the trend for the other two models. Compared to the results for the S2 simulations, the addition of land use in the S3 simulations strengthens the trend for all models. Thus the models agree that CO_2 and land-use causes an increase in the amplitude of the seasonal cycle at Mauna Loa but disagree about the effect of climate on the trend in the amplitude of the seasonal cycle at Mauna Loa.

4. Discussion

Analyses based on atmospheric data have contributed substantially to our understanding of the dynamics of the global

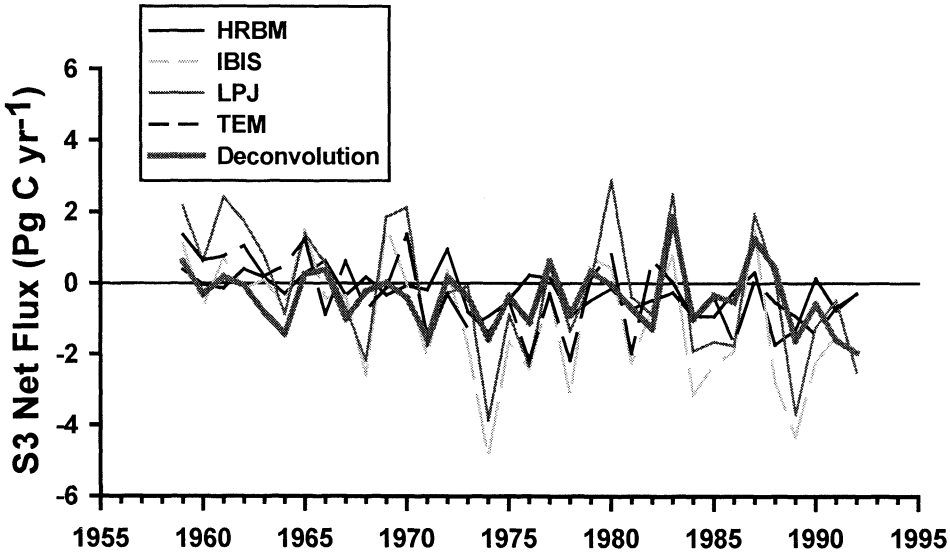

Figure 7. Interannual variability in net carbon exchange with atmosphere between 1958 and 1992 estimated by four terrestrial biosphere models (TBMs) in simulations which considered the simultaneous effects of increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment. The thick shaded line is the interannual variability estimated with a single deconvolution analysis that considered interannual variability in atmospheric carbon storage and estimates of releases to the atmosphere associated with fossil fuel emissions and the long-term trend in ocean uptake of atmospheric CO_2 (see section 2). Positive values indicate net releases to the atmosphere and negative values indicate net storage in terrestrial ecosystems.

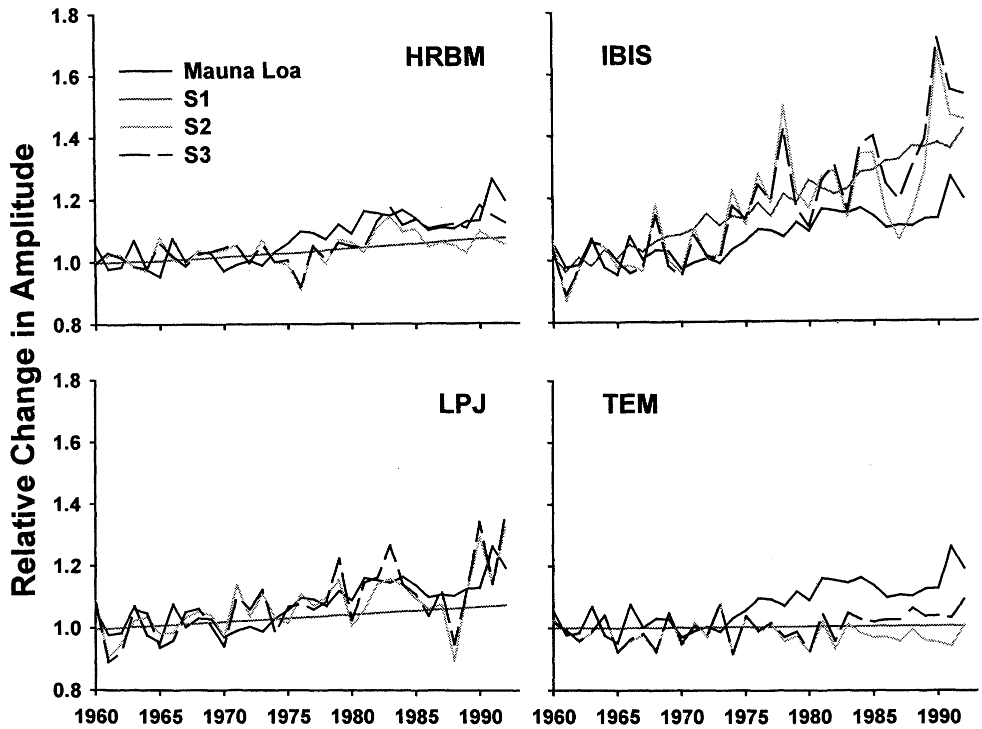

Figure 8. The trends in the amplitude of the seasonal cycle of atmospheric CO_2 at the Mauna Loa monitoring station between 1960 and 1992, relative to the amplitude between 1960 and 1964, as estimated using the fluxes of NPP and R_H simulated by each of four terrestrial biosphere models (HRBM, IBIS, LPJ, and TEM), compared with the trends estimated from the observations. The trends for each of three simulations are shown: increasing atmospheric CO_2 only, increasing atmospheric CO_2 and climate variability, and increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment.

Table 6. The Slope of the Change in the Amplitude of the Seasonal Cycle of Atmospheric CO_2 Observed at the Mauna Loa Monitoring Station Between 1960 and 1992 (Relative to the Amplitude in 1960) as Estimated from the Observations and as Estimated by Using the Fluxes of NPP and R_H Simulated by Each of Four Terrestrial Biosphere Models (HRBM, IBIS, LPJ, and TEM)

Model Observations	Slope, % yr^{-1} (0.63)	R^2
HRBM		
S1	0.26	0.84
S2	0.27	0.45
S3	0.52	0.66
IBIS		
S1	1.32	1.32
S2	1.29	0.74
S3	1.62	0.81
LPJ		
S1	0.25	0.84
S2	0.49	0.57
S3	0.65	0.64
TEM		
S1	0.03	0.84
S2	-0.04	0.07
S3	0.25	0.48

The slope for each of three simulations is shown: increasing atmospheric CO_2 only (S1), increasing atmospheric CO_2 and climate variability (S2), and increasing atmospheric CO_2, climate variability, and cropland establishment and abandonment (S3). The proportion of variation explained (R^2) is for regressions between the observed amplitude and simulated amplitude between 1960 and 1992.

carbon cycle over the last century. Long-term single and double deconvolution analyses based on ice core and atmospheric CO_2 data suggest that the terrestrial biosphere transitioned between releasing carbon to the atmosphere to storing carbon from the atmosphere during the 1950s [*Bruno and Joos,* 1997; *Joos and Bruno,* 1998]. More recent analyses based on CO_2 and O_2 data have informed us of the relative role of the terrestrial and oceanic systems in global carbon dynamics [*R. F. Keeling et al.,* 1996] and have provided some insight into the broad-scale latitudinal patterns of carbon exchange with the atmosphere [*Tans et al.,* 1990; *Ciais et al.,* 1995; *R. F. Keeling et al.,* 1996; *Heimann and Kaminski,* 1999; *Rayner et al.,* 1999; *Prentice et al,* 2000]. These analyses indicate that during recent decades, the tropics have been approximately neutral and that ecosystems north of the tropics have been sinks for atmospheric carbon [*Prentice et al.,* 2000]. Because of limitations in the data measured by the global network of CO_2 monitoring stations, analyses based on atmospheric data are not likely to yield substantial insight as to longitudinal patterns of carbon storage within latitudinal bands without information on additional constraints [*Prentice et al.,* 2000], and they currently provide no information on processes responsible for terrestrial sources and sinks. Simulations by TBMs complement analyses based on atmospheric data in that simulated sources and sinks are the result of mechanisms represented in the models. The simulations by TBMs also have the potential to provide additional constraints for atmospheric analyses if we have confidence in the patterns simulated by the models for certain regions. In this study we took the logical step of comparing simulations among TBMs driven by some of the major factors thought to be controlling terrestrial carbon dynamics: rising atmospheric CO_2, interannual climate variability, and cropland establishment and abandonment. Our overall goal in this analysis was to sharpen our thinking about confidence in the patterns simulated by TBMs and to reduce uncertainties by helping to focus attention on what additional steps are required for improving our understanding of processes represented in TBMs and for improving the data needed for driving and evaluating TBMs.

Over the long-term (1920-1992), all of the models' S3 runs yield a time history of terrestrial uptake that is consistent (within the uncertainty) with the long-term double deconvolution analysis (Figure 5), which indicates that terrestrial ecosystems transitioned from releasing carbon to the atmosphere during approximately the first half of the period (8.8 Pg C from 1920 to 1957) to storing carbon during the second half of the period (-14.3 Pg C from 1958 to 1992). Up to about 1960, three of four analyses indicate a net release of carbon from terrestrial ecosystems to the atmosphere (Table 4). In the simulations, cropland establishment is shown to be the dominant cause of this release. After about 1960, all analyses indicate a net uptake of carbon by terrestrial ecosystems. In the simulations, cropland establishment continues to release carbon, but this release is exceeded by uptake, partly because of the physiological effects of rapidly rising atmospheric CO_2. During the 1980s, the simulations indicate that terrestrial ecosystems stored between 0.3 and 1.5 Pg C yr^{-1}, which is within the uncertainty of analysis based on CO_2 and O_2 budgets (Figure 5). Three of the four models indicate (in accordance with O_2 evidence) that the tropics were approximately neutral while a net sink existed in the ecosystems north of the tropics. The temporal pattern of net carbon exchange simulated by the models is primarily associated with the relative effects of increasing atmospheric CO_2 and land use. It is important to note that the models have substantially different sensitivities to rising atmospheric CO_2 and that the range of sensitivities among the models has substantial implications for attempts to stabilize the atmospheric concentration of CO_2 [*Kicklighter et al.,* 1999a]. The comparisons with the long-term atmospheric analyses do not currently allow us to distinguish among the algorithms represented in the models with respect to controls over the response to rising atmospheric CO_2, and it is clear that each of the models is capable of achieving a closer match with the atmospheric analyses through minor adjustments of parameters that influence the sensitivity of NPP to increasing CO_2. Also, the sensitivity of the long-term response of net carbon storage may be associated, in part, with the sensitivity of decomposition to the increase in organic matter inputs to the soil [*Kicklighter et al.,* 1999a]. Thus additional effort will still be required to transfer the understanding gained from careful syntheses of whole-ecosystem CO_2 perturbation experiments to the models [*McGuire et al.,* 1995; *Pan et al.,* 1998], specifically from free-air CO_2 exchange (FACE) experiments [e.g., *DeLucia et al.,* 1999].

Among the models, the global releases associated with land use generally track the releases simulated by the bookkeeping model of *Houghton* [1999] from 1920 to about 1960 but diverge in the 1960s (Figure 6) when the expansion of croplands decelerates in the land use data set used to drive the models in this study (Figure 3). It is important to recognize that the land use analysis presented here is incomplete because it did not consider the conversion of forests to pastures and did not consider possible changes in harvest and regrowth cycles within managed forests. The marginal effect of land use change during the 1980s is estimated as releases of between 0.6 and 1.0 Pg C yr^{-1}, which is consistently lower than estimates of a bookkeeping model by *Houghton* [1999], which consider pasture conversion. Although the consideration of pasture conversion would likely lead to higher land use releases by the models in this study, there are also regional differences in the trajectory of croplands between *Houghton* [1999] and the land use data set of this study. These differences likely contributed to differences between the estimates of *Houghton* [1999] and the models in this study. Also, if the effects of rising CO_2 are stronger in regrowing forests than in mature forests, the net releases associated with cropland establishment and abandonment simulated by the process-based models may be smaller than those simulated by a bookkeeping model, which does not represent these effects. To evaluate this issue, we conducted land use only simulations with LPJ and TEM in which the models were driven by the spin-up level of atmospheric CO_2 and the same climate as in the S1 simulation. We found very little difference between the global and regional results of the land use only simulations and the marginal effect of land use calculated as the difference between the S3 and S2 simulations. This analysis suggests that enhanced carbon storage associated with increasing CO_2 in the S3 simulation was approximately compensated by enhanced carbon release associated with land use. Climate-related changes in the natural disturbance regime could also affect the carbon balance, but only one of the models (LPJ) implemented a climate-related natural fire regime. Thus we conclude that the primary difference between the land use fluxes estimated by *Houghton* [1999] and this study are associated with differences between the land use data sets used in the studies. To enhance the ability of models to more completely consider the effects of land use and land-cover change on terrestrial carbon storage, improvements in the data sets used to drive the models are required so that the data sets incorporate the timing, extent, and types of major disturbances influencing carbon storage.

Although all of the models indicate that substantial forest regrowth is occurring in ecosystems north of the tropics because of the legacy of cropland abandonment 50-100 years ago, the models disagree as to whether the carbon fluxes associated with agriculture are larger than the regrowth. Thus our analysis identified that the fluxes associated with agricultural production, harvest, and subsequent decomposition of agricultural products represents a major uncertainty among the models. Clearly, the models need to be enhanced so that they consider major crop types and management schemes. To apply the models with these enhancements will require the development of data sets that can identify the spatial extent of major crop types and management schemes through time.

Previous model comparisons at the global scale have evaluated the spatial and seasonal sensitivity of NPP to climate among TBMs [*Kicklighter et al.,* 1999b] but have not evaluated the long-term or interannual variability of carbon storage to historical climate trends and variability [but see *Schimel et al.,* 2000]. Although all of the models agree that the long-term effect of climate on carbon storage, as indicated by the difference between the S2 and S1 simulations, has been small relative to the effects of increasing atmospheric CO_2 and land use, the models disagree as to whether climate variability and change in the twentieth century has promoted carbon storage or release. For one of the models (HRBM), climate variability and change promoted storage, while it promoted release for two of the models (IBIS and LPJ). The simulation by the fourth model, TEM, indicated that climate promoted release before about 1960 and storage after 1960. An examination of the differences in NPP and decomposition between the S2 and S1 simulations indicates that there is variability in the sensitivity of NPP and decomposition to long-term trends in climate among the models; that is, in some of the models NPP is more sensitive to climate trends, while in other models decomposition is more sensitive. Also, previous work with TEM suggested that the storage after 1960 as indicated by the difference between the S2 and S1 simulations might be associated with an interaction between increasing CO_2 and climate in the S2 simulation, in which a warming climate increases the mineralization of nitrogen in soils and the uptake of nitrogen by vegetation that enhances the incorporation of elevated CO_2 into production [*Melillo et al.,* 1993] to more than compensate for releases of carbon from enhanced decomposition [see also *Shaver et al.,* 1992]. To evaluate this possibility, we conducted a climate-only simulation with TEM. The results of the simulation indicated that climate variability and change promoted release of carbon to the atmosphere after 1960, which suggests that the climate sensitivity of carbon storage may depend on interactions between the carbon and nitrogen cycles of ecosystems [see also *Vukicevic et al.,* 2001]. Thus the simulations in this study have revealed key uncertainties with respect to the sensitivity of carbon storage to climate variability and change. These uncertainties include (1) the relative effects of climate variability and change on NPP and decomposition and (2) the role of carbon and nitrogen interactions in the sensitivity of NPP and decomposition to climate variability and change.

These uncertainties in the climate sensitivity of NPP and decomposition are amplified in the comparison of interannual variability in net carbon exchange simulated by the models since 1958. If one assumes that the contribution of the ocean to interannual variability in the rate of increase of atmospheric CO_2 is small compared with terrestrial contributions (see *Lee et al.* [1998] and *Feely et al.* [1999], but see *Vukicevic et al.* [2001]), then the atmospherically based analysis of Figure 7 indicates that interannual variability in carbon storage in the terrestrial biosphere is largely related to variability in the El Niño/Southern Oscillation (ENSO) [see also *Keeling and Revelle,* 1985]. For example, the large releases from the terrestrial biosphere in 1983 and 1987 inferred from the single deconvolution are associated with ENSO activity that is characterized by warmer and drier conditions in the tropics. In the year or two following ENSO, e.g., 1984-1985 and 1988-1989, the tropics are characterized by a cooler and wetter climate that is referred to as La Niña. While the models tend to agree that ENSO years tend to promote the release of carbon to the atmosphere and La Niña years tend to promote the storage of carbon, there are substantial differences in the simulated net carbon exchange among the models related to the sensitivity of simulated NPP and decomposition to climate variability. The different sensitivities of NPP and decomposition among the models cannot be attributed to differences in hydrology as LPJ uses a two-layer bucket model and IBIS uses a six-layer finite-element model, yet the models have similar responses of NPP and decomposition to climate. Also, it is not clear if the variability is primarily driven by variation in temperature, by variation in precipitation, or by covariation in temperature and precipitation [*Tian et al.*, 1998, 2000; *Vukicevic et al.*, 2001]. Evaluation of model performance in the context of stand-level eddy covariance measurements has the potential to inform modifications of the models to improve the sensitivity of simulated processes to climatic variability and change. To be useful in this context, eddy covariance measurements must be continuous, must be conducted over several years to pick up the interannual and long-term responses of carbon storage to climate variability and change and must have ancillary measurements to help identify the sensitivity of the component fluxes of net ecosystem exchange with the atmosphere and the role of carbon and nitrogen interactions in the sensitivity of the component fluxes.

The changing amplitude of the seasonal cycle provides a constraint on the sum of all processes affecting NCE of the terrestrial biosphere in recent decades. The models vary in their ability to simulate the changing amplitude of the seasonal cycle of atmospheric CO_2 at the Mauna Loa monitoring station, which has increased between 1958 and 1992 (Figure 8). The relative change in the amplitude of the seasonal cycle based on the S1 simulations indicates that the trend is overestimated by IBIS and underestimated by the three other TBMs. The sensitivity of the trend in the amplitude growth to the magnitude of NCE in the S1 simulations among the models indicates that response of the terrestrial biosphere to increasing atmospheric CO_2 has the potential to explain the trend. The results of the S2 and S3 simulations suggest that climate and land use may also play a role. Taken together, the seasonal cycle results suggest that the observed trend may be a consequence of the effects of rising CO_2, climate variability, land use changes, or a combination of these effects. The possible influences of rising CO_2, climate change, and land-cover change on the amplitude of the seasonal cycle have been noted in previous analyses [*Kohlmaier et al.*, 1989; *C. D. Keeling et al.*, 1995, 1996; *Randerson et al.*, 1997, 1999; *Zimov et al.*, 1999]. Because our analysis suggests that multiple combinations of these factors may explain the increase in the amplitude of the seasonal cycle, testing the ability of models to reproduce changes in the seasonal cycle may not be sufficient for identifying how the representation of processes should be improved in the models. Additional experimentation with the models will be required to evaluate hypotheses concerning the role of these factors in controlling features of the seasonal cycle [e.g., see *McGuire et al.*, 2000b]. Also, the inability of models to reproduce changes in the seasonal cycle may be associated with factors not considered in our analysis.

It is also important to recognize that the models in this study did not consider anthropogenic nitrogen deposition. Anthropogenic nitrogen deposition may be contributing ~0.2-0.5 Pg C yr^{-1} to carbon storage [*Townsend et al.*, 1996; *Holland et al.*, 1997; *Nadelhoffer et al.*, 1999; *Lloyd*, 1999] but was not included in these experiments. Because anthropogenic nitrogen deposition is considered a major factor influencing carbon sequestration in ecosystems north of the tropics and may have substantial interactions with increasing atmospheric CO_2 and the regrowth of forests after cropland abandonment [*Schimel et al.*, 1996], it will be important to add this factor to the consideration of rising CO_2, climate variability, and land use in future studies.

In summary, the results presented here are consistent with atmospheric data and provide a first consistent quantitative partitioning of total terrestrial biosphere-atmosphere exchanges. They support the idea that the effects of tropical deforestation in the 1980s have been slightly more than counterbalanced by uptake in terrestrial ecosystems associated with the effects of rising CO_2. Our analyses have also identified some of the next steps for improving the process-based simulation of historical terrestrial carbon dynamics. These steps include (1) the transfer of insight gained from stand-level process studies to improve the sensitivity of simulated carbon storage responses to changes in CO_2 and climate, (2) improvements in the data sets used to drive the models so that they incorporate the timing, extent, and types of major disturbances, (3) the enhancement of the models so that they consider major crop types and management schemes, (4) development of data sets that identify the spatial extent of major crop types and management schemes through time, and (5) the consideration of the effects of anthropogenic nitrogen deposition. The evaluation of the performance of the models in the context of a more complete consideration of the factors influencing historical terrestrial carbon dynamics is important for reducing uncertainties in representing the role of terrestrial ecosystems in future projections of the Earth system.

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