The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO₂ in the United States

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ABSTRACT

We use the Terrestrial Ecosystem Model (TEM, Version 4.1) and the land cover data set of the international geosphere–biosphere program to investigate how increasing atmospheric CO_2 concentration and climate variability during 1900–1994 affect the carbon storage of terrestrial ecosystems in the conterminous USA, and how carbon storage has been affected by land-use change. The estimates of TEM indicate that over the past 95 years a combination of increasing atmospheric CO_2 with historical temperature and precipitation variability causes a 4.2% (4.3 Pg C) decrease in total carbon storage of potential vegetation in the conterminous US, with vegetation carbon decreasing by 7.2% (3.2 Pg C) and soil organic carbon decreasing by 1.9% (1.1 Pg C). Several dry periods including the 1930s and 1950s are responsible for the loss of carbon storage. Our factorial experiments indicate that precipitation variability alone decreases total carbon storage by 9.5%. Temperature variability alone does not significantly affect carbon storage. The effect of CO_2 fertilization alone increases total carbon storage by 4.4%. The effects of increasing atmospheric CO_2 and climate variability are not additive. Interactions among CO_2, temperature and precipitation increase total carbon storage by 1.1%. Our study also shows substantial year-to-year variations in net carbon exchange between the atmosphere and terrestrial ecosystems due to climate variability. Since the 1960s, we estimate these terrestrial ecosystems have acted primarily as a sink of atmospheric CO_2 as a result of wetter weather and higher atmospheric CO_2 concentrations. For the 1980s, we estimate the natural terrestrial ecosystems, excluding cropland and urban areas, of the conterminous US have accumulated 78.2 Tg C yr^{-1} because of the combined effect of increasing atmospheric CO_2 and climate variability. For the conterminous US, we estimate that the conversion of natural ecosystems to cropland and urban areas has caused a 18.2% (17.7 Pg C) reduction in total carbon storage from that estimated for potential vegetation. The carbon sink capacity of natural terrestrial ecosystems in the conterminous US is about 69% of that estimated for potential vegetation.

1. Introduction

Atmospheric CO_2 concentration has increased from around 275 ppmv in the eighteenth century to around 360 ppmv in the early 1990s due to

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fossil fuel combustion and land use change (Schimel et al., 1996a). The surface air temperature of the world has increased by 0.5°C since the middle of the 19th century (Jones et al., 1991). The instrumental records of climate also indicate substantial interannual and decadal variability in temperature and precipitation over the past century (Nicholls et al., 1996). Many ecosystem pro-

cesses that affect carbon exchange between terrestrial ecosystems and the atmosphere are sensitive to changes in climate and atmospheric CO_2 concentration (Dai and Fung, 1993, Goulden et al., 1996, Melillo et al., 1996, Post et al., 1997). The effect of changes in historical atmospheric CO_2 concentration and climate on terrestrial carbon storage, however, is inadequately understood (Post et al., 1997; King et al., 1997).

The response of ecosystem processes at regional and global scales to changing climate and atmospheric composition is a central theme in the analysis of global change. The traditional focus of ecology or biology, i.e., the organism-centered approach, lacks many of the technical tools for large-scale ecosystem analysis (Ehleringer and Field, 1993). Spatially-explicit models of ecosystem processes have become a key tool for the evaluation of the response of large-scale terrestrial ecosystems to changing climate and atmospheric composition (Melillo et al., 1996). Most modeling efforts in recent years have focused on understanding the equilibrium response of net primary productivity and carbon storage in terrestrial ecosystems to doubled atmospheric CO_2 and associated climate change (Melillo et al., 1993; Woodward et al., 1995; VEMAP Members, 1995; Heimann et al. 1997a). Only a few studies have attempted to investigate the interannual variations of terrestrial carbon fluxes and storage. Empirical models, e.g., various modifications of the Miami Model (Lieth, 1975), have initially been used to simulate the effect of historical climate variability on terrestrial carbon storage (Dai and Fung, 1993; Kaduk and Heimann, 1994). Post et al. (1997) further modified the Miami Model to include a CO_2 response term to investigate the combined effects of CO_2 fertilization and climate variability on the terrestrial carbon storage. The instantaneous responses of the equilibrium functions of these models do not account for ecosystem processes such as the feedbacks between the carbon and nitrogen cycles (McGuire et al., 1993), and may ignore lagged responses to climate change (Kindermann et al., 1996; Schimel et al., 1996b; Braswell et al., 1997). Recently, some process-based, spatially explicit biospheric models have been modified to examine the responses of terrestrial carbon storage to interannual climate variability (Kindermann et al., 1996) and historical atmospheric CO_2 concentration (Friedlingstein et al., 1995; Melillo et al., 1996; Kicklighter et al., 1999). To improve the application

of these models to assess carbon storage responses to projected changes in climate and atmospheric CO_2, it is important to elucidate the processes that are responsible for the dynamics of these models over regions where we have confidence in the spatially explicit historical climate variability.

In this study, we attempt to establish a basic understanding of processes controlling carbon storage change in natural terrestrial ecosystems as well as to explore changes in carbon storage capacity caused by land-use change. We use a transient version of the Terrestrial Ecosystem Model (TEM 4.1) to investigate the dynamics of terrestrial carbon fluxes and storage in potential vegetation of the conterminous USA during 1900–1994 in simulations with: (1) historical atmospheric CO_2 concentrations alone; (2) historical air temperature alone; (3) historical precipitation alone; (4) a combination of historical temperature and precipitation; and (5) a combination of historical atmospheric CO_2 concentrations with historical air temperature and precipitation. Then, we use the simulation results with the recent land cover data set (Loveland and Belward, 1997) of the international geosphere–biosphere program (IGBP) to examine how the conversion of natural ecosystems to cropland and urban areas has affected carbon flux and storage. We focus on the conterminous US for 3 reasons: (1) we have more confidence in the historical climate data of the conterminous US (Karl et al., 1994; Jones et al., 1991) because it is based on a rather dense monitoring network of weather stations; (2) we can compare our results to a previous study on the equilibrium response of terrestrial ecosystems in the conterminous US (VEMAP Members, 1995); and (3) historical changes in carbon storage have been assessed with inventory techniques for some sectors of the conterminous US (Turner et al., 1995). In addition, the contribution of various nations to sources and sinks of atmospheric CO_2 is an important issue in the negotiations of a global climate convention.

2. Methodology

2.1. Model description

The terrestrial ecosystem model (TEM) is a process-based biogeochemical model that uses spatially referenced information on climate, eleva-

tion, soils, and vegetation to make monthly estimates of important carbon and nitrogen fluxes and pool sizes (Fig. 1). The TEM has been used to examine patterns of net primary production (NPP) of terrestrial ecosystems in South America (Raich et al., 1991) and North America (McGuire et al., 1992, McGuire et al., 1993, VEMAP Members, 1995, Schimel et al., 1996, Pan et al., 1996). The model has also been used to estimate carbon storage and NPP responses of global terrestrial ecosystems to elevated atmospheric carbon dioxide and potential climate change (Melillo et al. 1993, 1995a; McGuire et al., 1995, 1997; Xiao et al., 1997). In most of the previous applications of TEM, the model was used to examine changes in carbon fluxes and pools based on equilibrium conditions (e.g., annual NPP equals annual heterotrophic respiration, annual N uptake by vegetation equals annual net nitrogen

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

mineralization, etc.). In this study we use version 4.1 of TEM to examine the transient responses of carbon fluxes and pools of natural vegetation in the conterminous US to historical atmospheric CO_2, air temperatures and precipitation during the time period between 1900 and 1994.

In TEM, the net carbon exchange between the terrestrial biosphere and the atmosphere is represented by net ecosystem production (NEP), which is calculated as the difference between net primary production (NPP) and heterotrophic respiration (R_H). Net primary production is calculated as the difference between gross primary production (GPP) and plant respiration (R_A). We describe the general formulations of the fluxes GPP, R_A, and R_H to identify the algorithms and feedbacks that are influenced by changes in atmospheric CO_2, temperature, and precipitation. Relevant details are provided in Section 7. Additional detailed descriptions of the structure, parameterization, calibration, and performance of the terrestrial ecosystem model have been documented in previous work (Raich et al., 1991; McGuire et al., 1992, 1993, 1995, 1997; Melillo et al., 1993, 1995; Pan et al., 1996, 1998; Xiao et al., 1997).

The flux GPP considers the effects of several factors and is calculated at each monthly time step as follows:

$$GPP = C_{max} f(PAR) f(LEAF) f(T) f(C_a, G_v) f(NA)$$

where C_{max} is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF is leaf area relative to maximum annual leaf area (phenology), T is temperature, C_a is atmospheric CO_2 concentration, G_v is relative canopy conductance, and NA is nitrogen availability. The effects of elevated atmospheric CO_2 directly affect $f(C_a, G_V)$ by altering intercellular CO_2 of the canopy (Pan et al., 1998; McGuire et al., 1997; see Section 7). Nitrogen availability also influences the ability of vegetation to incorporate elevated CO_2 into production (Pan et al., 1998; McGuire et al., 1997; see Section 7). In version 4.1 of TEM, elevated atmospheric CO_2 also decreases the nitrogen concentration of vegetation to influence the nitrogen requirements of production and decomposition (McGuire et al., 1997; see Section 7). Temperature directly influences $f(T)$, indirectly influences $f(LEAF)$ and $f(C_a, G_V)$ through effects on estimated evapotranspiration as well as potential evapotranspiration, and indirectly influences
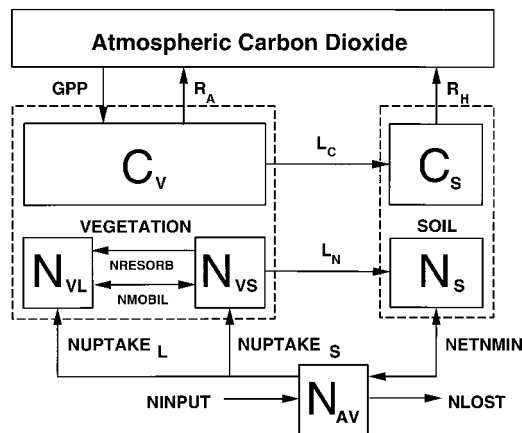
nitrogen availability through effects on the rates of nitrogen uptake, decomposition, and net nitrogen mineralization (see Section 7). Precipitation influences $f(\text{LEAF})$ and $f(C_a, G_V)$ through effects on estimated evapotranspiration and influences nitrogen availability through soil moisture effects on the rates of nitrogen uptake, decomposition, and net nitrogen mineralization (see Section 7).

In TEM, the flux R_A represents total respiration (excluding photorespiration) of living vegetation, including all CO_2 production from various processes including plant respiration, nutrient uptake, and biomass construction. In TEM, R_A is the sum of growth respiration, R_g, and maintenance respiration, R_m. Growth respiration is prescribed to be 20% of the difference between GPP and maintenance respiration (see Raich et al., 1991). Changes in atmospheric CO_2, temperature, and moisture influence growth respiration through effects on GPP. Temperature also influences growth respiration through effects on maintenance respiration. We model maintenance respiration as a direct function of plant biomass (C_V) as follows:

$$R_m = K_r(C_V)\, e^{rT},$$

where K_r is the per-gram-biomass respiration rate of the vegetation at $0°C$, C_V is the mass of carbon in the vegetation, T is mean monthly air temperature, and r is the instantaneous rate of change in respiration with change in temperature. The parameter r depends on temperature and is calculated as described in McGuire et al. (1992). In version 4.1 of TEM we added an algorithm that alters the parameter K_r to represent the accumulation of tissues with low metabolic rate such as heartwood in woody vegetation and structural carbon in non-woody vegetation (see Section 7).

In TEM, the flux R_H represents decomposition of all organic matter in an ecosystem and is calculated at a monthly time step as follows (Raich et al., 1991; McGuire et al., 1997).

$$R_H = K_d C_S f(M_V)\, e^{0.0693T},$$

where K_d is the heterotrophic respiration rate at $0°C$, C_s is carbon soil organic matter, M_V is mean monthly volumetric soil moisture and T is mean monthly air temperature. In version 4.1, changes in atmospheric CO_2 influence the parameter K_d, which is sensitive to increases in the carbon to nitrogen ratio of litterfall that are associated with elevated atmospheric CO_2 (McGuire et al., 1997,

see Section 7). Temperature directly influences R_H through effects on $e^{0.0693T}$. Both temperature and precipitation influence soil moisture to affect $f(M_V)$. Changes in CO_2 concentration, temperature, and precipitation also influence R_H through effects on NPP that affect the pool size of soil organic matter through changes in litterfall input (see Raich et al., 1991).

In earlier versions of TEM, the equilibrium calculations of 3 intermediate models were used as inputs to TEM (Pan et al., 1996). The intermediate models included an irradiance model, a water balance model (Vorosmarty et al., 1989), and a leaf phenology model (Raich et al., 1991). In version 4.1 of TEM, the algorithms of the intermediate models have been incorporated into TEM so that estimates of irradiance, water fluxes and pools, and leaf phenology are calculated simultaneously with the estimates of carbon and nitrogen fluxes and pools. Unlike previous versions, version 4.1 of TEM may be used to simulate either equilibrium or transient fluxes and pools of carbon, nitrogen, and water.

2.2. Application of the model

The application of TEM in either equilibrium or transient mode requires the input of atmospheric CO_2 concentration and 6 spatially explicit variables: vegetation, elevation, soil texture, mean monthly temperature, monthly precipitation, and mean monthly solar radiation. The spatially-explicit input data sets are gridded at a resolution of $0.5°$ latitude by $0.5°$ longitude. In transient mode, input data sets describing interannual variability in atmospheric CO_2 concentration, temperature and/or precipitation are required. In addition to the input data sets, TEM also requires soil- and vegetation-specific parameters appropriate to a grid cell. Although many of the parameters in the model are defined from published information, some of the vegetation-specific parameters are determined by calibrating the model to the fluxes and pool sizes of an intensively studied field site. The data used to calibrate the model for different vegetation types are documented in previous work (Raich et al., 1991; McGuire et al., 1992, 1995). The parameterization used in this study is the same as the TEM parameterization used in VEMAP Members (1995), except for the new

parameters added to version 4.1 (see McGuire et al., 1997 and Section 7).

To apply TEM to a transient scenario of atmospheric CO_2 and/or climate, it is first necessary to run the model to equilibrium with a long-term baseline climate appropriate to the initial year of the simulation. The baseline run for each grid cell starts with the December values from the appropriate vegetation-specific calibration. To determine a solution for baseline conditions, the model is run with an open nitrogen cycle so that nitrogen is annually imported or exported through the inorganic nitrogen pool depending on whether soil organic matter is nitrogen poor or rich in comparison with the target C to N ratio of soil at the calibration site. Each grid cell in the baseline simulation is determined to have reached equilibrium when the annual fluxes of NPP, litterfall carbon (L_C) and heterotrophic respiration (R_H) differ by less than $1 \, g \, C \, m^{-2} \, yr^{-1}$; those of net nitrogen mineralization (NETNMIN); litterfall nitrogen (L_N); and nitrogen uptake by vegetation (NUPTAKE) differ by less than $0.02 \, g \, N \, m^{-2} \, yr^{-1}$; and annual nitrogen inputs (NINPUT) and losses (NLOST) from the ecosystem are less than $0.01 \, g \, N \, m^{-2} \, yr^{-1}$. To run a grid cell in transient mode, the initial values of the pools for the grid cell are set to the December values of the equilibrium baseline solution for the grid cell and the model is run with the temporal variation in climate and atmospheric CO_2 for the transient scenario.

To apply TEM to a transient scenario, the nitrogen cycle can be open or closed. To run TEM with an opened nitrogen cycle, spatially-explicit data of nitrogen input are required. Presently, spatially explicit data of nitrogen deposition for the time period from 1900 to 1994 are not generally available. Thus, in this study we closed the nitrogen cycle during the transient simulations so that there is no nitrogen imported or exported from the grid cell. Although no nitrogen is imported or exported, nitrogen can be redistributed between soil and vegetation during the transient simulation.

2.3. Baseline input data

The baseline input data we used in this study are from the VEMAP data sets, with the exception of long-term mean temperature and precipitation.
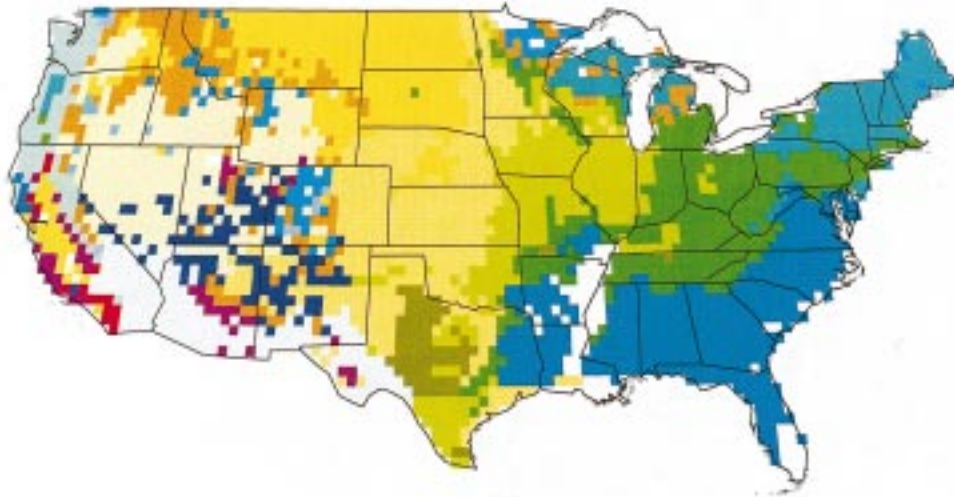
The details of the VEMAP data sets are described by Kittel et al. (1995). The baseline vegetation data set is required to define the vegetation-specific parameters for each grid cell in the application of TEM. In this study, we use the VEMAP vegetation distribution for the conterminous US (Fig. 2), which is based on Kuchler (1964, 1975). The vegetation types in the VEMAP data set are classified on the basis of physiognomic characteristics of dominant lifeforms except for grassland vegetation types, which are distinguished by photosynthetic pathway (C_3 versus C_4). As in VEMAP Members (1995), a single C_3 grassland parameterization was used in the application of TEM to both C_3 and C_4 grasslands.

The VEMAP soils data set is based on the Kern (1995) 10-km gridded Soil Conservation Service National Soil database (NATSGO). The data were aggregated to $0.5°$ resolution and grouped by cluster analysis to a set of 1 to 4 modal soils. The first modal soil was used to represent soil properties for the grid cell. The TEM uses soil texture, characterized by the percentage of sand, silt and clay (Kittel et al., 1995; VEMAP Members, 1995). Elevation data are used to affect snowmelt and therefore affect soil moisture. The elevation data used in this study represent an aggregation to $0.5°$ resolution of the NCAR/NAVY global 10-min elevation data set (NCAR/NAVY, 1984).

The baseline temperature data are developed from the temperature anomalies of Jones et al. (1991) and the long-term temperatures of the Cramer and Leemans CLIMATE database (Cramer and Leemans, 1991; Cramer, personal communication) by the Max-Planck Institute for Meteorology. First, the monthly temperature anomalies from 1900 to 1930 were used to develop "long-term" monthly mean temperature anomalies. Then, the "long-term" mean temperature anomalies were added to the long-term monthly air temperatures of the CLIMATE database to generate the baseline temperature data. The missing data were filled before interpolating to $0.5° \times 0.5°$ spatial resolution (Heimann et al. 1997b).

The baseline precipitation data are developed from the precipitation anomalies of Hulme (1995) and the long-term precipitation data of the Cramer and Leemans CLIMATE database by the Max-Planck Institute for Meteorology. First, the monthly precipitation anomalies from 1900 to 1930 were

VEMAP VEGETATION DATA SET

LEGEND

Temp. Mixed Xeromorphic Wood.
Tropical Evergreen Forest
Tropical Deciduous Forest
Temperate Deciduous Forest
Warm Temp. Mixed/Everg. Forest
Cool Temp. Mixed Forest
Continental Temp. Conifer Forest
Maritime Temp. Conifer Forest
Boreal Forest
Tundra

Subtropical Arid Shrublands
Temperate Arid Shrublands
Mediterrean Shrublands
C4 Grasslands
C3 Grasslands
Tropical Deciduous Savanna
Temperate Conifer Savanna
Warm Temperate/S.T. Mixed Savanna
Temperate Deciduous Savanna
Tropical Thorn Woodland
Temp. Conifer Xeromorphic Wood.

Fig. 2. Potential vegetation distribution of the conterminous US based on VEMAP vegetation classification (VEMAP Members 1995).
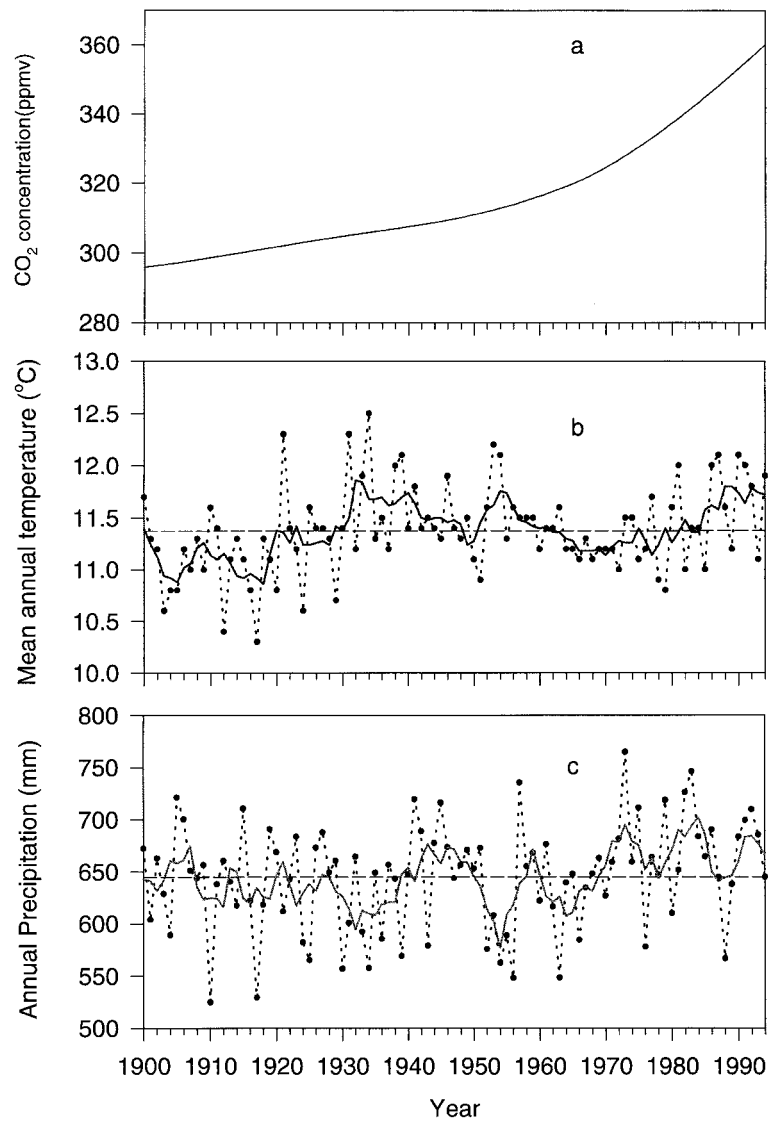
Fig. 3. Historical variations in (a) global mean annual atmospheric CO_2 concentrations; (b) mean annual temperature; and (c) annual precipitation for the conterminous US. The heavy line shows 5-year running mean.

used to develop "long-term" monthly mean precipitation anomalies. The "long-term" precipitation anomalies were used to develop monthly change ratios which were then multiplied by the appropriate monthly precipitation of the CLIMATE data

to generate the baseline precipitation data. The missing data were filled before interpolating to $0.5° \times 0.5°$ spatial resolution (Heimann et al., 1997b). The anomalies for the baseline were restricted to the period 1900–1930 because we assumed that

Fig. 4. Historical variations in annual mean temperature anomalies (relative to 1961–1990 reference period) for biomes in the conterminous US. The heavy line shows 5-year running mean.
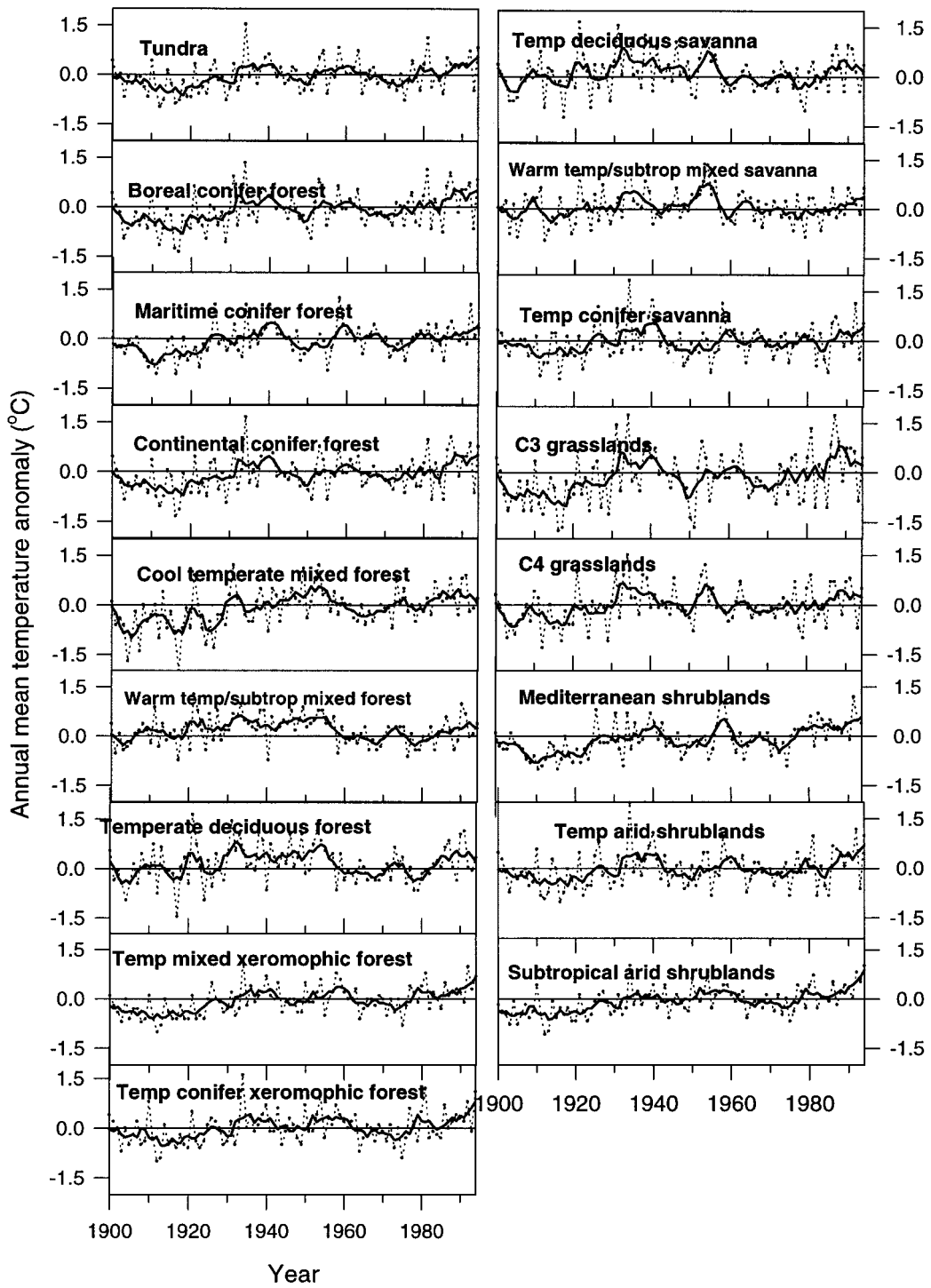
these anomalies were more characteristic of an equilibrium climate prior to 1900 than anomalies from later in the simulation period.

The VEMAP monthly mean solar radiation data (Kittel et al., 1995; VEMAP Members, 1995) are derived from daily solar radiation data estimated by the CLIMSIM model (Running et al., 1987; Glassy and Running, 1994), which uses latitude, elevation, the diurnal range of temperature, and the occurrence of precipitation. To generate solar radiation data, the CLIMSIM model used the elevation data set described earlier and daily temperature and precipitation data sets from VEMAP (Kittel et al., 1995; VEMAP Members, 1995).

2.4. Transient input data

The historical mean atmospheric CO_2 concentration data used in this study (Fig. 3a) were generated from ice core data and atmospheric CO_2 observations (Enting et al., 1994). Atmospheric CO_2 concentrations increased from 296 ppmv in 1900 to 361 ppmv in 1994. For this study, we do not consider the spatial variability of atmospheric CO_2 concentration. Thus, the same atmospheric CO_2 concentration is used for each grid cell during each month.

The gridded historical temperature data $(0.5° \times 0.5°)$ are developed from the temperature anomalies of Jones et al. (1991) and the long-term temperatures of the Cramer and Leemans CLIMATE database (Cramer and Leemans, 1991; Cramer, personal communication) in a similar manner to the generation of the baseline temperature data. In the resulting historical data set, substantial interannual and decadal variations occur in annual mean temperature for the conterminous US (Fig. 3b). There are three warming periods: 1930s-1940s, 1950s and 1980s. The temperature data also show two distinct cooling periods: one extending from 1900 to 1930, another extending from 1960 to the late 1970s. The temporal pattern of interannual variations in annual mean temperature also varies across biomes (Fig. 4).

The gridded historical precipitation data $(0.5° \times 0.5°)$ are developed from the precipitation anomalies of Hulme (1995) and the long-term precipitation of the Cramer and Leemans CLIMATE database (Cramer and Leemans 1991; Cramer, personal communication) in a similar

manner to the generation of the baseline precipitation data. Again, substantial variations occur in annual precipitation data of the resulting data set (Fig. 3c). There are two wet periods: one is in the 1940s and another that extends from 1970 to 1994. The remaining periods were relatively dry, including the "Dust Bowl" period of the 1930s. Again, the temporal pattern of interannual variations in annual precipitation also varies across biomes (Fig. 5).

2.5. Experimental design

We designed a series of five experiments in this study (Table 1) to examine the sensitivity of terrestrial carbon fluxes and storage in potential vegetation of the conterminous US to historical atmospheric CO_2 concentrations, air temperatures and precipitation during the time period from 1900 to 1994. In experiment I, the atmospheric CO_2 concentrations between 1900 and 1994 were used as inputs to TEM to examine the effects of increasing CO_2 alone on terrestrial carbon fluxes and pools. This experiment also used the long-term mean temperature and precipitation data for the time period from 1900 to 1930 generated from the gridded historical temperature and precipitation data sets described above. In experiment II, the historical temperatures between 1900 and 1994 were used as TEM inputs to examine the effects of temperature variability alone on terrestrial carbon fluxes and pools. This experiment also used a constant atmospheric CO_2 concentration of 296 ppmv (i.e., the atmospheric CO_2 concentration at the beginning of 1900) throughout the study period, and the long-term mean precipitation data for the time period from 1900 to 1930 generated from the gridded historical precipitation data set described above. In experiment III, the historical precipitation between 1900 and 1994 were used as TEM inputs to examine the effects of precipitation variability alone on terrestrial carbon fluxes and pools. This experiment also used a constant atmospheric CO_2 concentration of 296 ppmv throughout the study period, and the long-term mean temperature data for the time period from 1900 to 1930. In experiment IV, the historical temperatures and precipitation between 1900 and 1994 were used as TEM inputs to examine the effects of temperature and precipitation variability on terrestrial carbon fluxes and
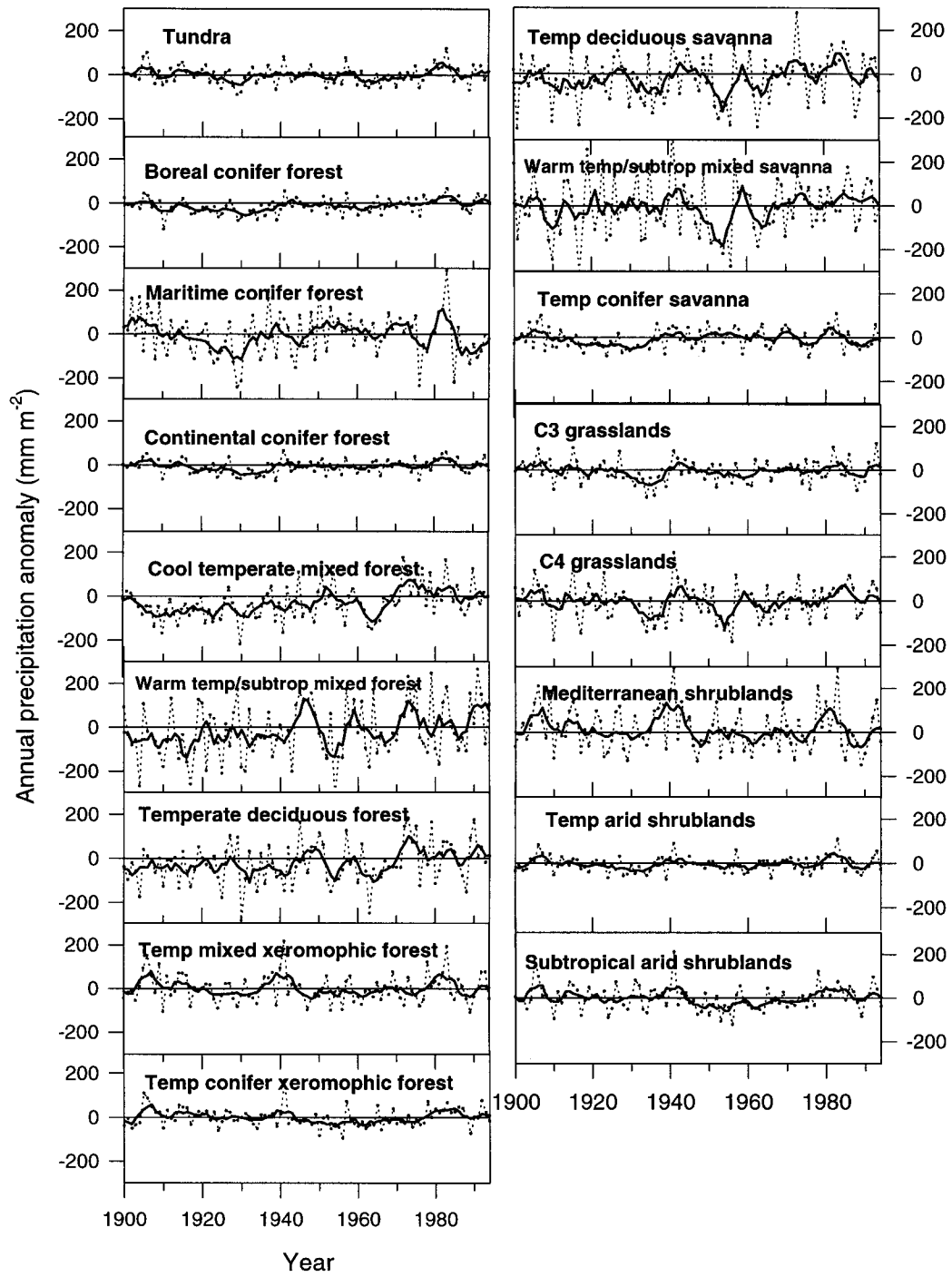
Fig. 5. Historical variations in annual precipitation anomalies (relative to 1961–1990 reference period) for biomes in the conterminous US. The heavy line shows 5-year running mean.

Table 1. *Design and data sources for 5 simulation experiments*

Experiment	CO_2	Temperature	Precipitation	Other variables[a]
I	historical	mean[b]	mean[c]	VEMAP datasets
II	constant[d]	historical	mean[c]	VEMAP datasets
III	constant[d]	mean[b]	historical	VEMAP datasets
IV	constant[d]	historical	historical	VEMAP datasets
V	historical	historical	historical	VEMAP datasets

[a] Other variables include mean solar radiation, elevation, soil texture and vegetation types of the VEMAP data sets (Kittel et al., 1995; VEMAP Members, 1995).
[b] Temperature in experiment I and III is long-term mean monthly temperature derived from gridded historical temperature data as described in text.
[c] Precipitation in experiment I and II is long-term mean monthly precipitation derived from gridded historical precipitation data as described in text.
[d] Atmospheric CO_2 concentration in experiment II, III and IV is 296 ppmv, which is CO_2 concentration level at the beginning of 1900 and remains unchanged during time period examined.

pools. This experiment also used a constant atmospheric CO_2 concentration of 296 ppmv throughout the study period. In experiment V, we used the historical CO_2 concentrations of experiment I, historical temperature data of experiment II and historical precipitation data of experiment III to examine the combined effects of increasing atmospheric CO_2 concentrations, and climate (temperature and precipitation) variability on carbon fluxes and pools. All the experiments used the VEMAP data sets described above for inputs of solar radiation, elevation, soil and vegetation data. For all five experiments, the terrestrial ecosystems in the conterminous US were assumed to be in equilibrium before 1900. TEM 4.1 first runs in equilibrium mode to generate the equilibrium baseline of carbon flux and storage using the long-term mean monthly climate and an atmospheric CO_2 concentration of 296 ppmv before starting the transient simulation.

There is no well-accepted procedure for initializing a transient simulation. One commonly used approach is to run a model to equilibrium using long-term average or mean climate (Kindermann et al., 1996). An alternative approach is to run a model repeatedly with a time series of historical climate until the model reaches equilibrium. It is not clear which method is preferable. We chose the former one.

2.6. Evaluating effects of clearing for cropland and urban areas on carbon storage

We used the recent global land cover data of the International Geosphere-Biosphere Program (IGBP) with the TEM results of simulation experiment V to evaluate how the conversion of natural ecosystems to cropland and urban areas affected carbon fluxes and storage in terrestrial ecosystems of the conterminous US. The IGBP land cover data set was based on 1-km AVHRR data spanning April 1992, through March 1993, which represents the state of land cover in the early 1990s. To match the resolution of our other spatially-explicit data bases, we aggregated the IGBP land cover data base to a resolution of $0.5°$ longitude and $0.5°$ latitude by calculating the percentage of cropland and urban areas in each $0.5° \times 0.5°$ grid cell (Fig. 6). Based on this land cover data set, we estimate that cropland and urban areas represent about 21% and 1%, respectively, of total land area in the conterminous US in 1992–1993.

To make a first order estimate on the effects of clearing natural areas for cropland and urban areas on carbon storage of the conterminous US, we assumed that the conversion of natural ecosystems to cropland and urban areas causes the loss of all vegetation carbon and half of reactive soil organic carbon. As most croplands cover only a portion of a $0.5°$ grid cell, we first determine the area of a grid cell covered by croplands and urban areas. Then, we multiply this area by the density of vegetation carbon and one half of the density of reactive soil organic carbon in the grid cell to determine the flux of carbon caused by human disturbance. Since our approach does not account for time series of land-use change, our analysis does not include the effect of abandoned croplands and forest regrowth on carbon storage.
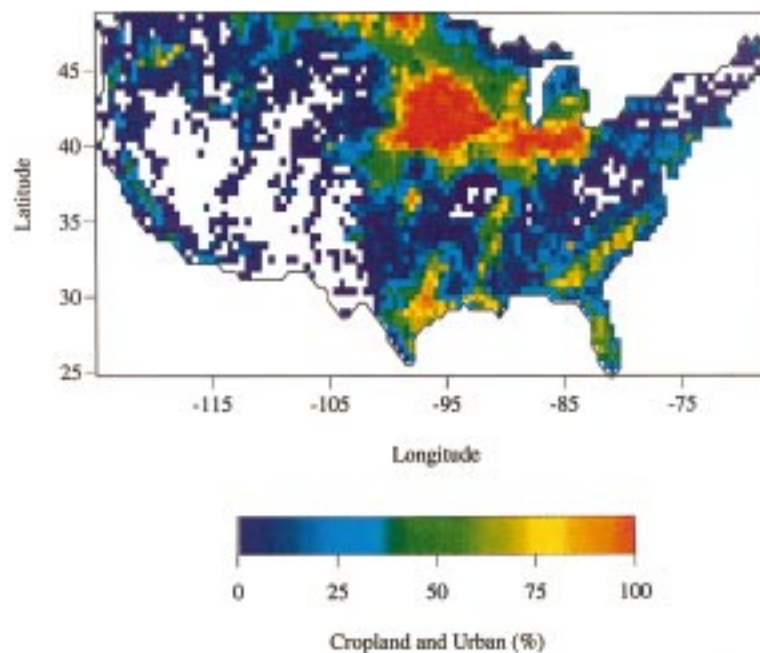
Fig. *6*. The extent of cropland and urban areas in the conterminous US in 1992–1993. This dataset represents the relative area of cropland and urban areas in a grid cell with a resolution of 0.5° longitude × 0.5° latitude. The dataset was derived from the IGBP global land cover dataset (Loveland and Belward, 1997), which was based on 1-km AVHRR data spanning April 1992 through March 1993.

3. Results

Based on the TEM equilibrium simulation, we suggest that the baseline for both annual NPP and annual R_H for potential vegetation in the conterminous US before 1900 was 3298×10^{12} g C (Tg C) yr^{-1}. The baseline for total carbon storage was 103×10^{15} g C (Pg C); 58 Pg C in vegetation and 45 Pg C in reactive soil organic matter (Table 2). In this analysis, we did not include biologically unreactive soil carbon, which was estimated to be 40% of total soil organic carbon (Melillo et al., 1995; McGuire et al., 1997). With this baseline, we then investigated the transient effects of CO_2 fertilization, climate variability and their combination on terrestrial carbon storage.

3.1. Transient effect of CO$_2$ fertilization

In response to historical atmospheric CO_2 concentration alone (experiment I), the TEM simulation indicates that the total carbon storage in potential vegetation of the conterminous US increases by 4.5 Pg C (4.4%) over the past 95 years, with 3.5 Pg C stored in vegetation and 1.0 Pg C stored in soil organic matter (Table 2). Total carbon storage increases across all biomes in the conterminous US as a result of CO_2 fertilization. The increases varied from +1.7% in cool temperate mixed forest to +13.8% in subtropical arid shrubland (Table 3). The biomes that increased carbon storage by more than +10% include temperate mixed xeromophic forest, temperate conifer xeromophic forest, warm temperate/subtropical mixed savanna, mediterranean shrublands and subtropical arid shrublands. Version 4.1 of TEM predicts that these biomes are very responsive to increasing atmospheric CO_2 because the enhancement of intercellular CO_2 is greater under dry conditions, which causes higher rates of carbon assimilation (Pan et al., 1998). This mechanism is consistent with the observation of enhanced water use efficiency in empirical studies (Bazzaz, 1990; Mooney et al., 1991). Other biomes are less responsive to increasing atmospheric CO_2 concentration.

Table 2. *Continental-scale responses of vegetation carbon, reactive soil organic carbon and total carbon storage to changes in atmospheric CO₂ concentration and climate variability during 1900–1994*

	Vegetation C (10^{15} g C)	Reactive soil organic C (10^{15} g C)	Total C (10^{15} g C)
baseline	58	45	103
CO₂	3.5 (+6%)	1.0 (+2%)	4.5 (+4.4%)
temperature	−0.3 (−0.5%)	0.1 (+0.1%)	−0.2 (−0.2%)
precipitation	−5.2 (−8.9%)	−4.6 (−10.2%)	−9.7 (−9.5%)
climate[a]	−5.2 (−8.9%)	−4.4 (−10.2%)	−9.6 (−9.3%)
total effects	−1.1 (−1.9%)	−3.2 (−7.2%)	−4.3 (−4.2%)
interaction[b]	0.9 (+1.5%)	0.3 (+0.7%)	1.2 (+1.1%)

[a] Indicates the combination of temperature and precipitation.
[b] Indicates the interactions among CO₂ temperature and precipitation.

In version 4.1 of TEM, all grasslands are parameterized as C_3 grasses. The carbon storage response of these grasslands is less than 4%. The modest response occurs because TEM predicts that the production responses of grasslands to elevated CO₂ are substantially limited by nitrogen availability in addition to water availability. Because of nitrogen limitation, grasslands do not substantially benefit from increased water use efficiency.

The continuous increase in carbon storage for potential vegetation in the conterminous US between 1900 and 1994 is a consequence of the lagged response of R_H to increasing atmospheric CO₂ concentration in relation to NPP (Fig. 7, also see Melillo et al., 1996 and Kicklighter et al., 1999). Thus, relatively more carbon is stored in terrestrial ecosystems each year as atmospheric CO₂ concentration increases. For the conterminous US, the overall increases of annual NPP and annual R_H during 1900–1994 are +6.7% and +3.9%, respectively. The difference between NPP and R_H, also known as net ecosystem production or NEP, shows a continuous increase over time, with a large growth rate of NEP since the late 1960s. For the 1980s, the TEM simulation indicates that the effects of CO₂ fertilization on carbon storage to be $113 \text{ g C m}^{-2} \text{ yr}^{-1}$ for potential vegetation in the conterminous US.

3.2. Transient effect of temperature variability

Based on the TEM simulation, we conclude that temperature variability alone (experiment II) has not induced a substantial change in total carbon storage for potential vegetation in the conterminous US over the past 95 years (Table 2). Although most biomes showed a decrease in total carbon storage, the range in biome response was quite small, and varied from −4.7% in temperate coniferous xeromophic forest to +1.2% in warm temperate/subtropical mixed forest (Table 3). Biomes had different responses over the simulation period because of different sensitivities to changes in temperature (McGuire et al., 1993) and because of spatial variation in the temporal pattern of temperature (Fig. 4).

The interannual patterns of both NPP and R_H show substantial year-to-year fluctuations (Fig. 8), which are associated with interannual and decadal temperature variations over the study period (Figs. 3b, 4). In response to these temperature variations, the balance between annual NPP and annual R_H changes to cause periods when the terrestrial ecosystems of the US are sources of atmospheric carbon (i.e., negative NEP) and other periods when these ecosystems are carbon sinks (i.e., positive NEP). Higher temperatures in the 1930's, for example, induced a larger increase in annual R_H than annual NPP so that the terrestrial ecosystems of the US were losing carbon to the atmosphere. Conversely, relatively lower temperatures in the period of 1900–1920 reduced annual R_H such that NPP was greater than R_H and terrestrial ecosystems of the US were gaining carbon. Although the overall change in carbon storage of potential vegetation was small, interannual and decadal variations in carbon fluxes were substantial (Fig. 8). The net carbon flux for potential vegetation in the conterminous US varied

Table 3. *Changes in total carbon storage induced by historical atmospheric CO_2 concentration, air temperatures, precipitation and their combination during 1900–1994*

Biomes	Area 10^{12} m^2	Baseline (g C m^{-2})	CO_2 (%)	Temperature (%)	Precipitation (%)	Climate[a] (%)	Interaction[b] (%)	Total effect (%)	Total effect (Tg C)
1 tundra	0.021	6759	2.6	−3.9	−3.7	−7.0	0.8	−4.2	−6.0
2 boreal conifer forest	0.164	18427	5.5	−0.3	−3.7	−4.9	−2.8	−1.3	−39.3
3 maritime conifer forest	0.208	16489	3.4	−0.5	−2.4	−2.9	0.8	1.3	44.6
4 continental conifer forest	0.488	13296	4.0	−0.5	−4.4	−4.9	0.7	−0.2	−13.0
5 cool temperate mixed forest	0.418	24333	1.7	−1.1	−3.5	−4.6	0.2	−2.7	−274.6
6 warm temp/subtrop mixed forest	0.958	25394	4.8	1.2	−9.4	−7.7	1.5	−1.9	−462.2
7 temperate deciduous forest	0.883	30440	3.7	−0.1	−9.3	−9.6	0.0	−5.7	−1532.1
10 temperate mixed xeromophic forest	0.113	5295	12.5	−2.3	−10.0	−11.5	1.7	1.9	11.4
11 temperate conifer xeromophic forest	0.262	5611	13.6	−4.7	−13.6	−16.0	2.1	−2.5	−36.8
13 temperate deciduous savanna	0.693	17440	4.5	−1.5	−18.1	−18.5	2.8	−12.3	−1486.6
14 warm temp/subtrop mixed savanna	0.173	9975	10.9	0.5	−28.2	−26.0	3.6	−13.3	−229.5
15 temperate conifer savanna	0.018	4355	3.1	0.1	−8.1	−7.6	3.4	−1.5	−53.4
17 C3 grassland	0.817	5708	5.1	0.3	−2.1	−2.2	1.5	4.8	−4.9
18 C4 grassland	1.041	4754	3.9	−0.2	−11.3	−10.6	3.3	−4.2	−207.9
19 mediterranean shrublands	0.038	6023	11.3	−1.7	−9.9	−10.8	0.9	0.6	1.4
20 temperate arid shrublands	0.794	3094	7.0	−0.8	−6.5	−7.7	1.5	1.3	31.9
21 subtropical arid shrublands	0.424	2020	13.8	−2.1	−16.1	−18.1	2.8	−1.6	−13.7
	7.511	13642	4.4	−0.2	−9.5	−9.4	1.1	−4.2	−4303.5

[a] Indicates the combination of temperature and precipitation.
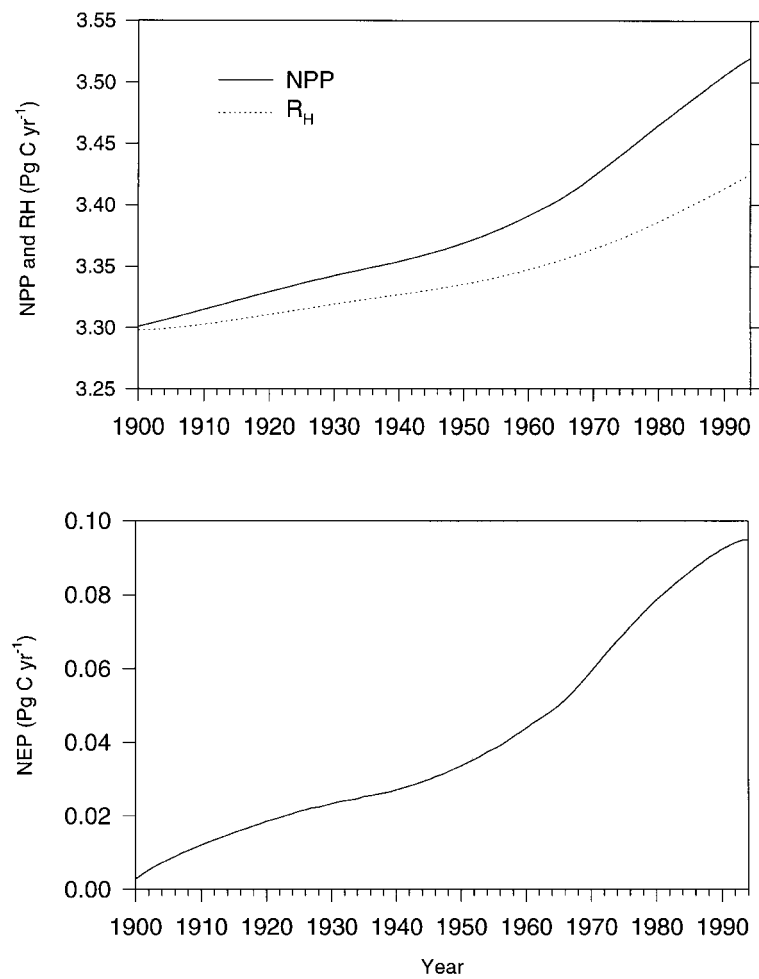[b] Indicates the interactions among CO_2, temperature and precipitation.

Fig. 7. Interannual variations in net primary production (NPP), heterotrophic respiration (R_H) and net ecosystem production (NEP) in the conterminous US induced by historical atmospheric CO_2 concentrations alone during 1900–1994.

from a maximum carbon release (0.3 Pg C) in 1934 to a maximum carbon uptake (0.3 Pg C) in 1946.

For potential vegetation of the conterminous US, increases in temperature tend to increase NPP, R_H, net nitrogen mineralization (NMIN), and EET, but tend to decrease volumetric soil moisture (M_V) (Fig. 9). Although the variability explained by temperature is much higher for R_H (Fig. 9; $R = 0.84$, $P < 0.0001$, $N = 95$) than for NPP (Fig. 9; $R = 0.38$, $P = 0.0002$, $N = 95$), the variability in responses is approximately the same for NPP and R_H (Figs. 8, 9; NPP: standard devi-

ation $= 0.10$ Pg C; R_H: standard deviation $=$ 0.08 Pg C). The high correlation between R_H and temperature indicates that the direct effects of temperature on R_H tend to predominate over the effects of temperature in decreasing M_V.

Because the continental-scale NPP is very highly correlated with GPP, defined as total carbon capture in photosynthesis ($R = 0.94$, $P < 0.0001$, $N = 95$) over the simulation period, the response of NPP to temperature can be interpreted in the context of GPP responses to temperature. The fact that the variability in NPP explained by temperature is low indicates that the
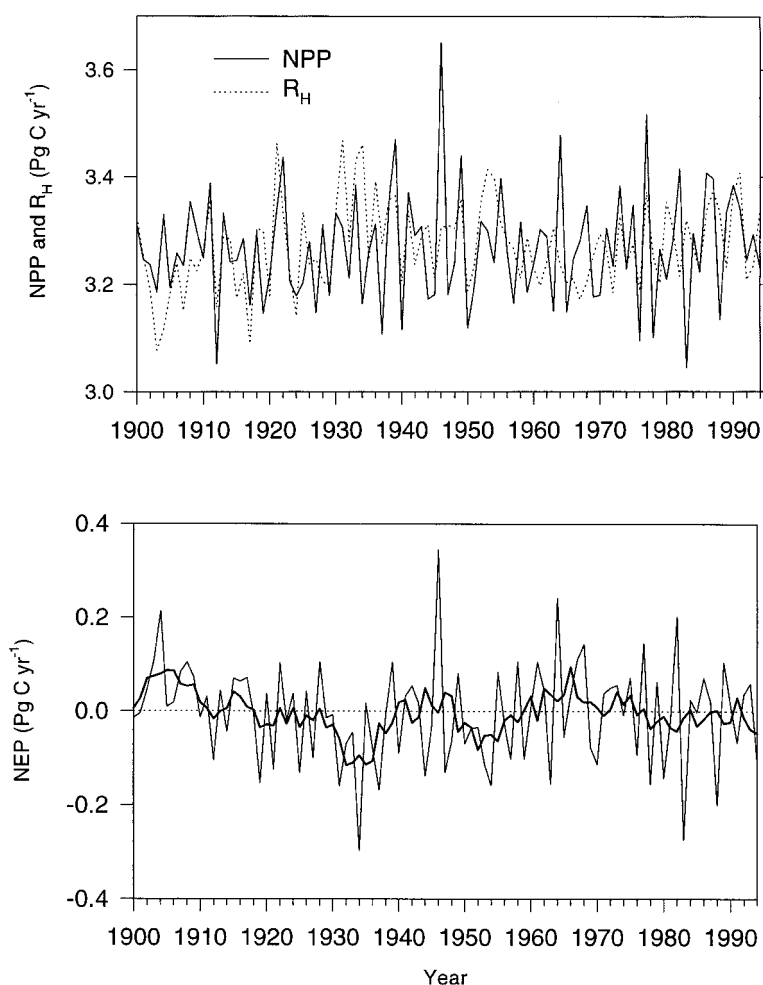
Fig. 8. Interannual variations in net primary production (NPP), heterotrophic respiration (R_H) and net ecosystem production (NEP) in the conterminous US induced by historical air temperatures alone during 1900–1994. Heavy line shows 5-year running mean.

interaction among temperature and processes influencing GPP is complex. The positive response of NPP indicates that the direct response of GPP to increased temperature and the effect of temperature in increasing nitrogen availability tend to be stronger than the effects of temperature in decreasing soil moisture. The variability in the response of NPP is primarily explained by variability in NMIN (Fig. 10; $R = 0.88$, $P < 0.0001$, $N = 95$), although NPP is also correlated with EET (Fig. 10; $R = 0.52$, $P < 0.0001$, $N = 95$). The tight coupling between NPP and NMIN, and the correlation between the response of NMIN and R_H

(Fig. 10; $R = 0.62$, $P < 0.0001$, $N = 95$) indicate that the positive response of NPP to increased temperature occurs primarily through higher rates of decomposition that enhance nitrogen availability through increased NMIN.

It should be noted that the correlation analyses conducted here did not explicitly consider the possible effect of temporal autocorrelation. To explore the potential importance of the autocorrelation issue for our conclusions, we performed autocorrelation analyses for the major variables over the 95-year time period. We found no meaningful autocorrelation. Therefore, we conclude that
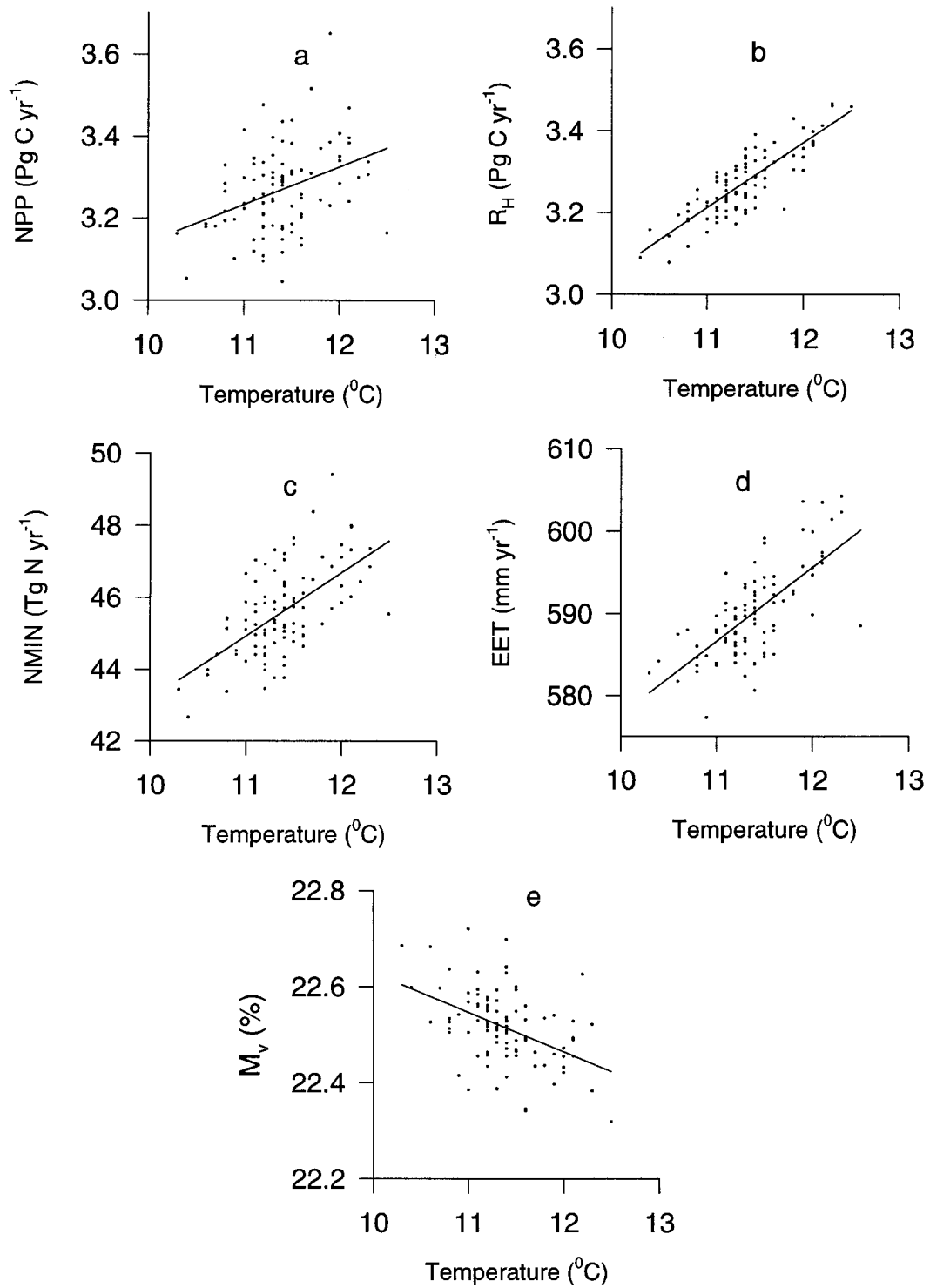
the highly significant correlations we have found demonstrate strong associations between important biogeochemical variables at the continental level.

3.3. Transient effect of precipitation variability

In response to historical precipitation variability alone (experiment III), the TEM simulation indicates that total carbon storage in potential vegetation of the conterminous US decreased by 9.7 Pg C (9.5%); a 5.2 Pg C (8.9%) decrease in the vegetation carbon, and a 4.6 Pg C (10.2%) decrease in the soil organic carbon (Table 2). The responses of total carbon storage among biomes ranged from -2.1% in temperate coniferous savanna to -28.2% in warm temperate/subtropical mixed savanna (Table 3). Biomes had different responses because of different sensitivities to changes in precipitation (Melillo et al., 1993) as well as spatial variation in the temporal pattern of precipitation (Fig. 5). For example, temperate deciduous forest and warm temperate/subtropical mixed forest had a substantial decrease in total carbon storage because of more frequent decreases in precipitation (Fig. 5). For similar reasons, temperate deciduous savanna and warm temperate/subtropical mixed savanna had larger decreases in total carbon storage than temperate conifer savanna.

Between 1900 and 1994, terrestrial ecosystems in the conterminous US experienced substantial variability in precipitation (Figs. 3c, 5). NPP was clearly more sensitive to changes in precipitation than R_H (Figs. 11, 12). Substantial decreases in precipitation occurred in the 1930s and 1950s. During these periods of sustained low precipitation, terrestrial ecosystems are sources of atmospheric CO_2. In contrast, during wet years such as 1957, terrestrial ecosystems are a sink of atmospheric CO_2. As a result of interannual precipitation variability, the net carbon flux estimated by TEM for potential vegetation in the conterminous

US varied from a maximum source of atmospheric CO_2 (1.8 Pg C yr^{-1}) in 1936 to a maximum sink of atmospheric CO_2 (1.0 Pg C yr^{-1}) in 1957 (Fig. 11). These interannual variations in net carbon flux are 3 to 6 times greater than comparable fluctuations caused by historical temperature variability. Since the early 1970s, the climate of the conterminous US has tended to be wet. Annual NPP in most years of the past two decades was greater than annual R_H so that terrestrial ecosystems in the conterminous US, as represented by potential vegetation, have recently been a sink of atmospheric CO_2.

For the conterminous US, increases in precipitation are: (1) strongly associated with increases in EET and M_V (2) moderately associated with increases in NPP and NMIN; and (3) weakly associated with increases in R_H (Fig. 12). The precipitation sensitivity of NPP was much higher than the precipitation sensitivity of R_H (Figs. 11, 12). In comparison to the temperature sensitivity of NPP, the variability of NPP responses to historical precipitation was much higher (compare Figs. 8, 11; temperature: standard deviation = 0.10 Pg C; precipitation: standard deviation = 0.49 Pg C). In contrast, the variabililty in R_H responses is approximately the same for historical temperature and precipitation (temperature: standard deviation = 0.08 Pg C; precipitation: standard deviation = 0.08 Pg C). Thus, the high interannual variability in NEP responses to historical precipitation is primarily caused by the high sensitivity of NPP to historical precipitation variability.

Because the continental-scale NPP is very highly correlated with GPP ($R = 0.99$, $P < 0.0001$, $N = 95$) over the simulation period, the response of NPP to precipitation can be interpreted in the context of GPP responses to precipitation. The response of NPP to increasing precipitation is: (1) very tightly coupled with NMIN (Fig. 13; $R = 0.89$, $P < 0.0001$, $N = 95$); (2) moderately coupled

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Fig. 9. The correlation of changes in mean annual temperature with annual changes in net primary production (NPP), heterotrophic respiration (R_H), net nitrogen mineralization (NMIN), estimated evapotranspiration (EET), and volumetric soil moisture (M_v) in the conterminous US induced by temperature variability during 1900–1994: (a) The relationship between annual mean temperature and annual NPP ($R = 0.38$); (b) The relationship between annual mean temperature and annual R_H ($R = 0.84$); (c) The relationship between annual mean temperature and annual NMIN ($R = 0.60$); (d) The relationship between annual mean temperature and annual EET ($R = 0.70$); (e) The relationship between annual mean temperature and annual M_v ($R = -0.44$).
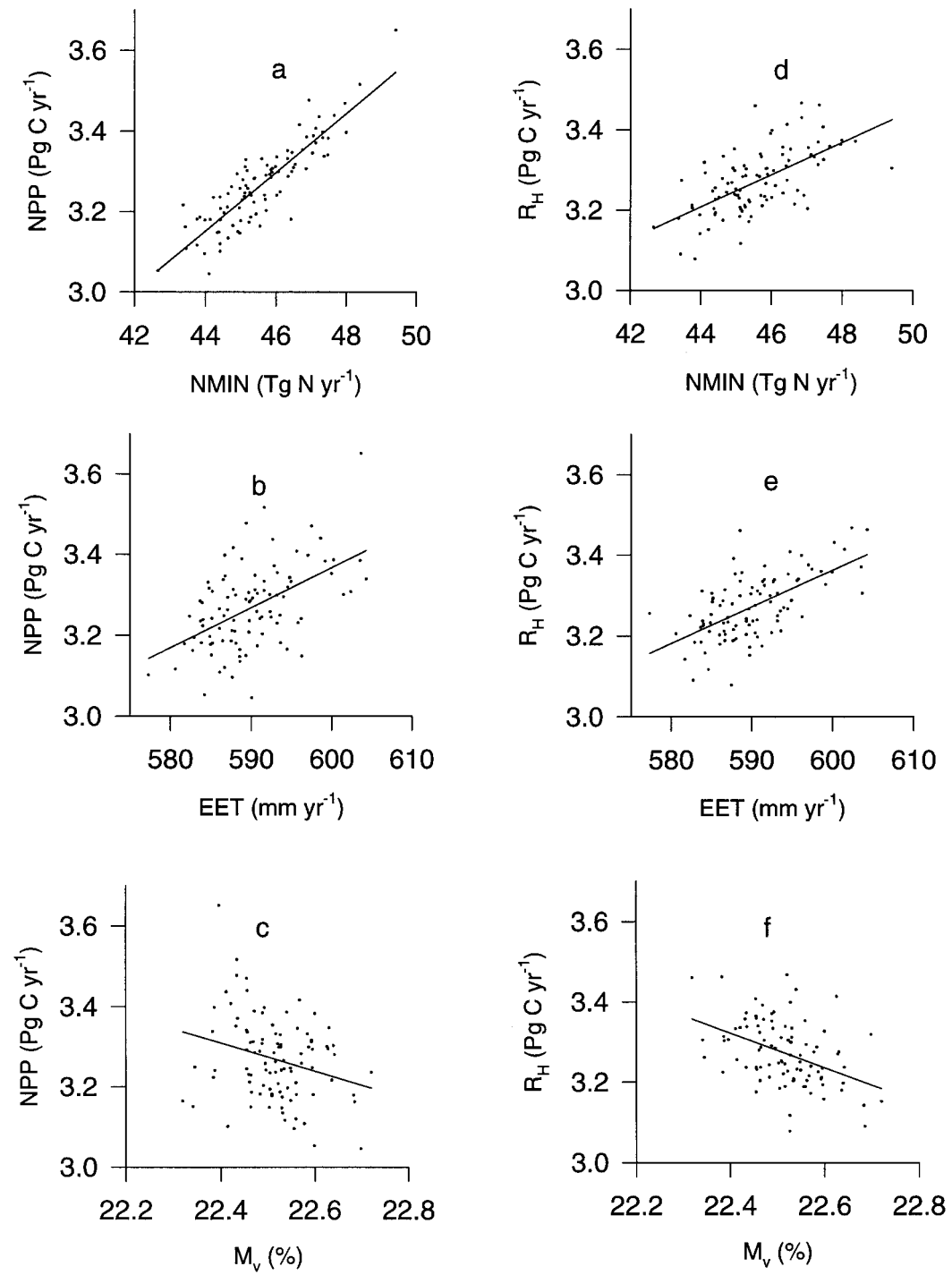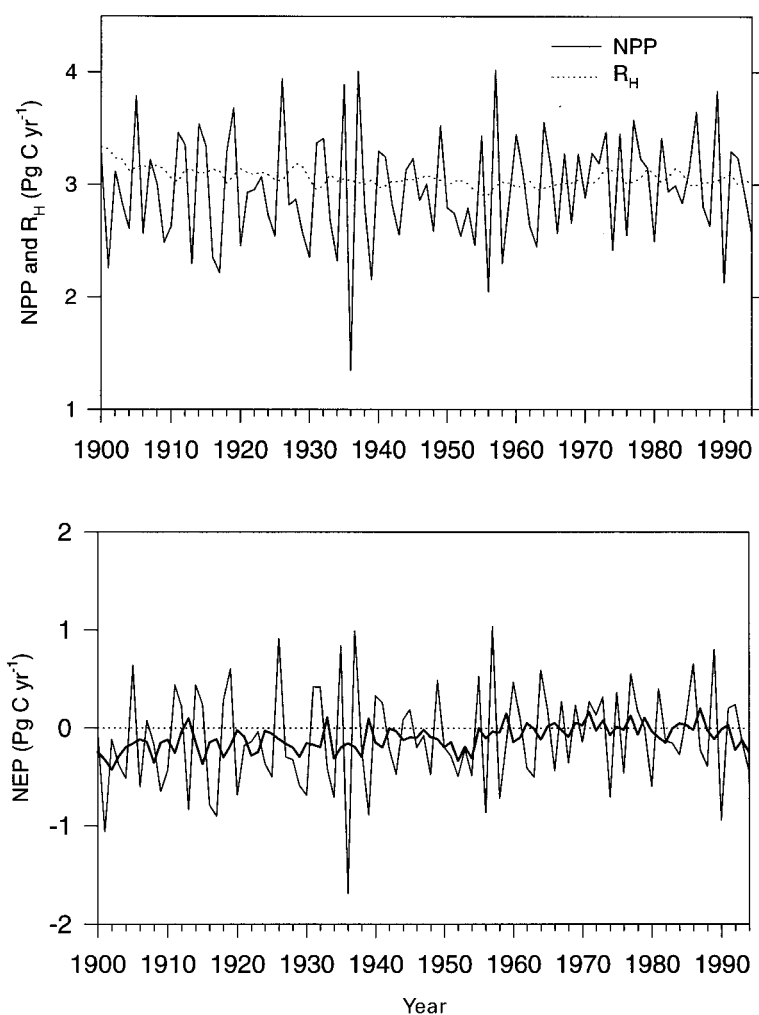
Fig. 11. Interannual variations in net primary production (NPP), heterotrophic respiration (R_H) and net ecosystem production (NEP) in the conterminous US induced by historical precipitation alone during 1900–1994. Heavy line shows 5-year running mean.

with EET (Fig. 13; $R = 0.52$, $P < 0.0001$, $N = 95$); (3) and weakly coupled with M_V (Fig. 13, $R = 0.34$, $P = 0.0006$, $N = 95$). These analyses indicate that nitrogen availability is the dominant process controlling production, although EET, which influences canopy conductance and canopy intercellular CO_2, also plays an important role. In addition, EET also influences leaf phenology to

Fig. 10. The relationship of annual NPP and annual R_H to annual changes in NMIN, EET and M_v in the conterminous US induced by temperature variability during 1900–1994: (a) The relationship between annual NPP and annual NMIN ($R = 0.88$); (b) The relationship between annual NPP and annual EET ($R = 0.52$); (c) The relationship between annual NPP and annual M_v ($R = -0.27$); (d) The relationship between annual R_H and annual NMIN ($R = 0.62$); (e) The relationship between annual R_H and annual EET ($R = 0.61$); (f) The relationship between annual R_H and annual M_v ($R = -0.43$).
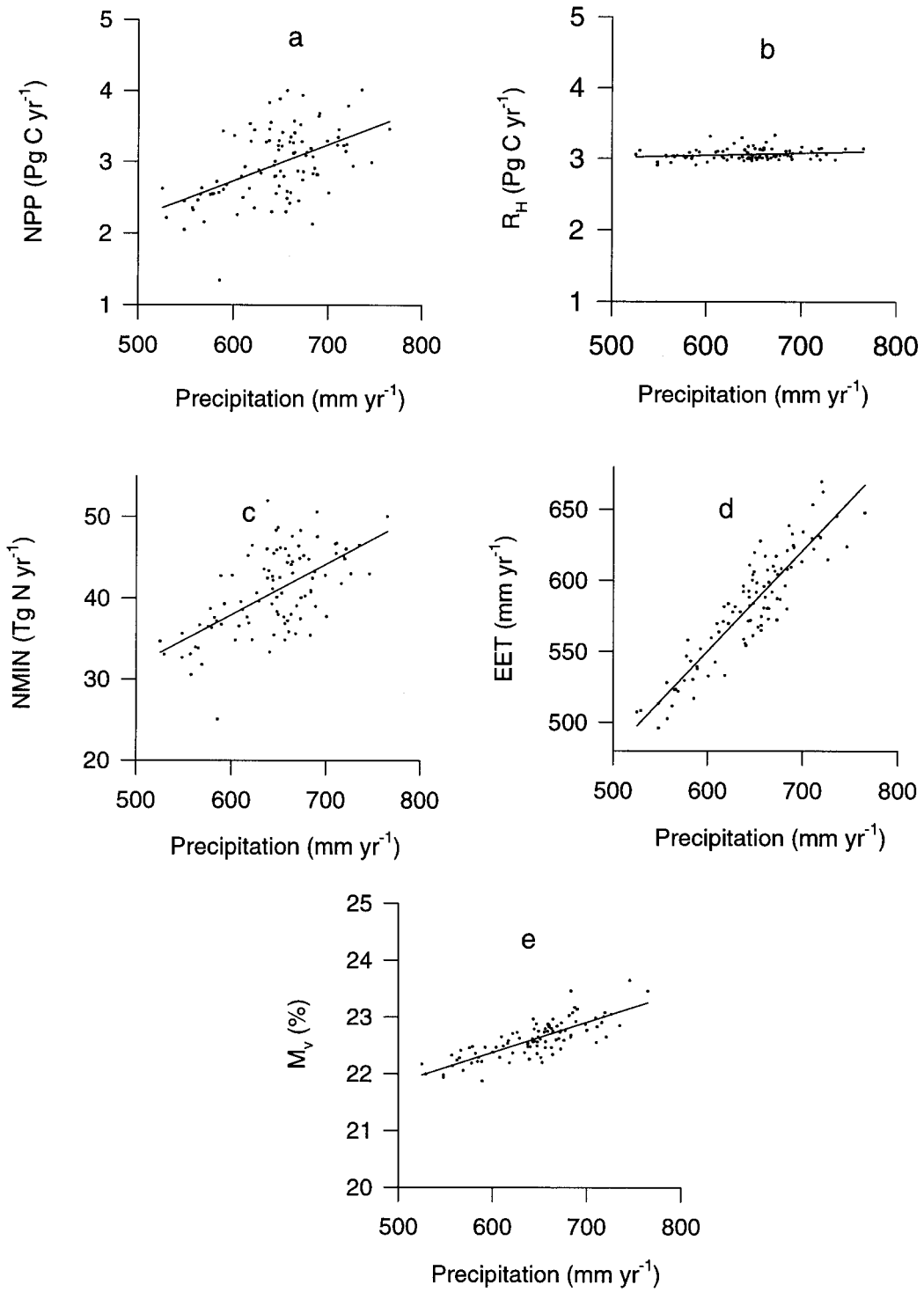
affect NPP. The weaker correlation of NPP with M_V probably occurs because increases in soil moisture influence NMIN by simultaneously influencing both gross nitrogen mineralization and nitrogen immobilization; NMIN is moderately correlated with increases in M_V ($R = 0.52$, $P < 0.0001$, $N = 95$).

3.4. Transient effect of climate variability

In response to a combination of historical air temperature and precipitation (experiment IV), TEM estimated that changes in vegetation carbon, soil organic carbon and total carbon storage for potential vegetation in the conterminous US over the past 95 years were very similar to the responses of carbon storage to historical precipitation (Table 2). Because simulated NPP is substantially more sensitive to changes in precipitation than to changes in temperature, the interannual patterns of NPP and NEP for the combination of historical temperature and precipitation were also very similar to the patterns for historical precipitation alone.

The combined effects of changes in air temperature and precipitation are similar to those resulting from precipitation alone; that is, decreases in precipitation lead to decreases in carbon storage (Table 3). In tundra, the combination of historical temperature and precipitation variability caused twice as much carbon to be released as the response for historical precipitation variability alone because carbon storage in tundra is about equally sensitive to historical temperature and historical precipitation variability (Table 3). In other biomes such as warm temperate/subtropical mixed forest, less carbon is released because temperature variability tended to increase carbon storage in this biome (Table 3) and partially compensated the carbon losses caused by precipitation variability.

3.5. Transient effect of climate variability and increasing atmospheric CO_2

In response to a combination of historical temperature, precipitation and atmospheric CO_2 concentration (experiment V), TEM estimates that for the period 1900–1994, total carbon storage in potential vegetation of the conterminous US decreased by 4.3 Pg C (4.2%), with a 1.1 Pg C (1.9%) decrease in vegetation carbon and a 3.2 (7.2%) decrease in soil organic carbon (Table 2). Our factorial experiments indicate that historical precipitation variation over the past 95 years was primarily responsible for the loss of carbon storage. The effect of CO_2 fertilization increased carbon storage by 5.3 Pg C (4.4%), but it did not compensate completely for the climate-induced carbon loss. The overall response of carbon storage to a combination of the three factors is not completely explained by simply adding together the individual effects attributed to CO_2 fertilization, temperature and precipitation variations. The interactions among historical atmospheric CO_2, temperature and precipitation accounted for an additional 1.2 Pg C carbon storage, with 0.9 Pg C stored in vegetation carbon and 0.3 Pg C stored in soils.

The timing and magnitude of annual NPP and annual R_H in response to the combination of climate and CO_2 are very similar to those observed in experiment III, where only precipitation was allowed to change over the study period (Fig. 14). Thus, in the combined experiment, precipitation explains most of interannual variability in NPP. Interannual variability in NPP and R_H led to substantial interannual variability in net carbon exchange between the atmosphere and terrestrial ecosystems, as represented by potential vegetation, with a maximum carbon release of 1.8 Pg C yr^{-1} in 1936 and a maximum carbon uptake of 1.1 Pg C yr^{-1} in 1957 (Fig. 14). Before 1960, the TEM results indicate that terrestrial ecosystems

Fig. 12. The correlation of changes in annual precipitation with annual changes in NPP, R_H, NMIN, EET, and M_v in the conterminous US induced by precipitation variability during 1900–1994: (a) The relationship between annual precipitation and annual NPP ($R = 0.52$); (b) The relationship between annual precipitation and annual R_H ($R = 0.22$); (c) The relationship between annual precipitation and annual NMIN ($R = 0.61$); (d) The relationship between annual precipitation and annual EET ($R = 0.91$); (e) The relationship between annual precipitation and annual M_v ($R = 0.80$).
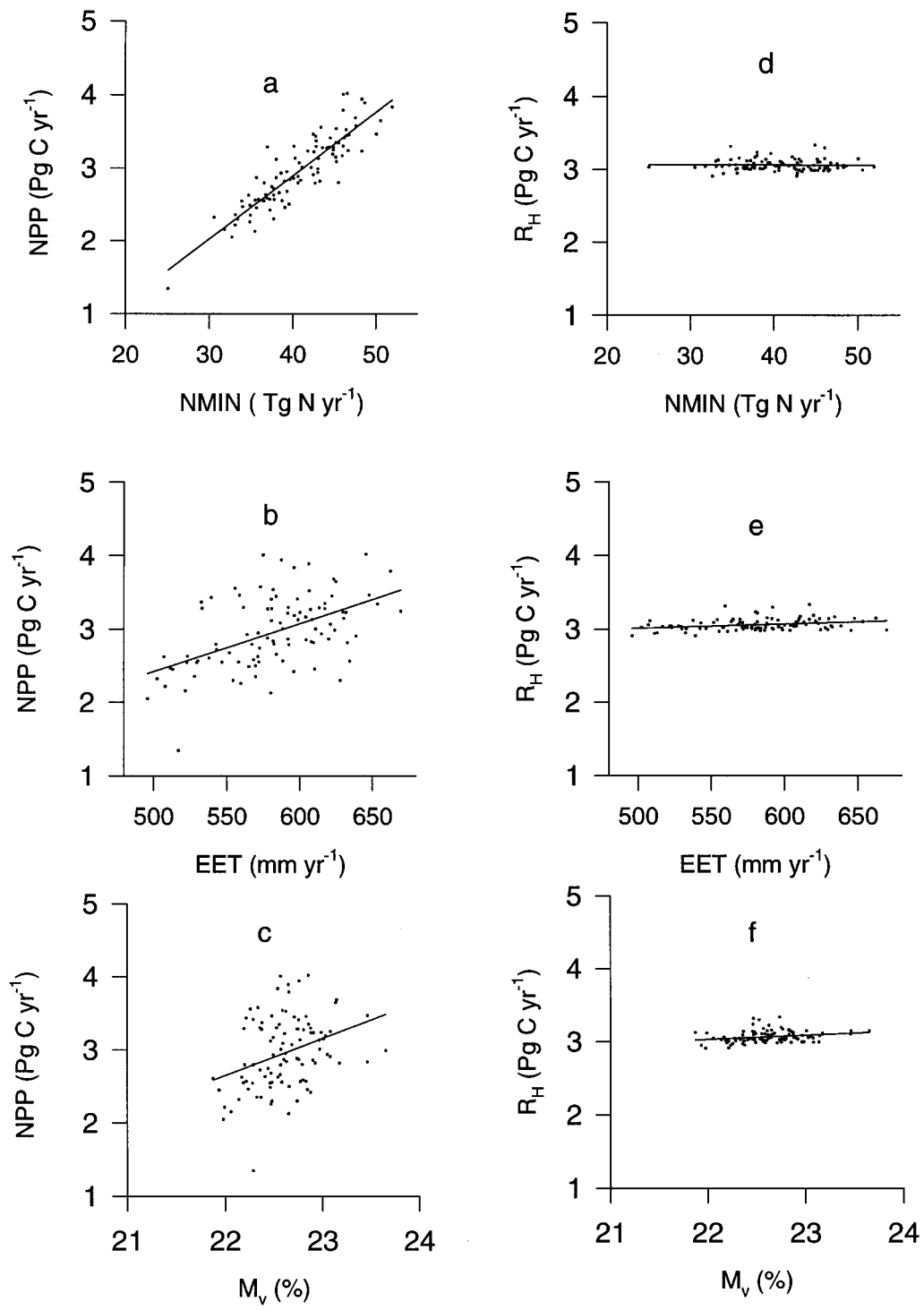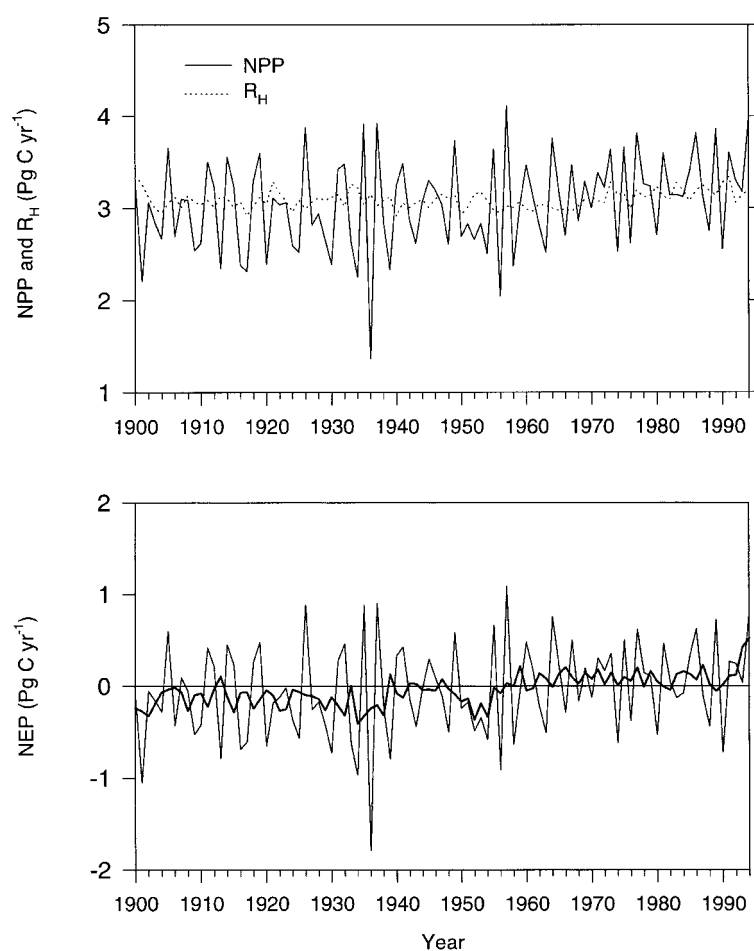
Fig. 14. Interannual variations in net primary production (NPP), heterotrophic respiration (R_H) and net ecosystem production (NEP) in the conterminous US induced by a combination of historical atmospheric CO_2 concentration, air temperature and precipitation. Positive NEP indicates a source of atmospheric CO_2. Negative NEP indicates a sink of atmospheric CO_2. Heavy line shows 5-year running mean.

in the conterminous US tended to be a source of atmospheric CO_2. Since 1960, terrestrial ecosystems of the conterminous US have been a carbon sink because of a wetter climate and the growth of atmospheric CO_2 concentration.

In response to a combination of historical cli-mate variability and increasing CO_2, total carbon storage of potential vegetation decreased in most biomes (Table 3). The largest relative decreases in carbon storage occurred in warm temperate/sub-tropical mixed savanna (-13%) and temperate deciduous savanna (-12.3%) because of more

Fig. 13. The relationship of annual NPP and annual R_H to annual changes in NMIN, EET and M_v in the conterminous US induced by precipitation variability during 1900–1994: (a) The relationship between annual NPP and annual NMIN ($R = 0.89$); (b) The relationship between annual NPP and annual EET ($R = 0.52$); (c) The relationship between annual NPP and annual M_v ($R = 0.34$); (d) The relationship between annual R_H and annual NMIN ($R = -0.01$); (e) The relationship between annual R_H and annual EET ($R = 0.29$); and (f) The relationship between annual R_H and annual M_v ($R = 0.25$).

frequent decreases in precipitation as well as the sensitivity of these biomes to dry weather (Fig. 5). Carbon storage has increased in five biomes. These increases, which ranged from $+0.6\%$ in Mediterranean shrubland to $+4.8\%$ in temperate conifer savanna, were caused by low variation in rainfall and the benefits of increased water use efficiency associated with elevated CO_2 in these dry biomes. All biomes show a general increase in NEP since 1960 (Fig. 15). Interannual variability in NEP differs across biomes. For example, NEP in temperate deciduous forest was more variable than in other forest biomes. In temperate deciduous savanna and warm temperate/subtropical mixed savanna, NEP was more variable than in temperate conifer savanna.

The carbon dynamics of a few biomes have a large influence on the overall changes in carbon storage of terrestrial ecosystems in the conterminous US during the time period from 1900 to 1994. The largest decreases in carbon storage occurred in temperate deciduous forest (about -1.5 Pg C) and temperate deciduous savanna (about -1.5 Pg C). These two biomes together represent 70% of the total loss in carbon storage for the conterminous US.

Similar to the positive correlation among temporal changes in NPP, NMIN, and EET for the conterminous US, NPP, NMIN, and EET are correlated for the aggregation of forest, savanna, and grassland vegetation types (Fig. 16). In each of these generalized vegetation types, NPP and NMIN are very tightly coupled: forests ($R = 0.83$, $P < 0.0001$, $N = 95$); savanna ($R = 0.90$, $P < 0.0001$, $N = 95$) and grassland ($R = 0.96$, $P < 0.0001$, $N = 95$). Although NPP and EET are moderately correlated in each of these three generalized vegetation types, the correlation is stronger in savanna ($R = 0.62$, $P < 0.0001$, $N = 95$) than forest ($R = 0.49$, $P < 0.0001$, $N = 95$) and grassland ($R = 0.47$, $P < 0.0001$, $N = 95$). Similarly, the correlation between NMIN and EET is stronger in savanna ($R = 0.71$, $P < 0.0001$, $N = 95$) than forest ($R = 0.57$, $P < 0.0001$, $N = 95$) and grassland ($R = 0.52$, $P < 0.001$, $N = 95$). In the VEMAP equilib-

rium simulations of TEM for contemporary climate, there are strong correlations between spatial changes in NPP, NMIN and EET (Schimel et al., 1997). Although our study indicates that there are also significant correlation between temporal changes in NPP, NMIN and EET, the correlations among temporal changes in these estimates are not as strong as the correlation among spatial changes. One possible reason for the difference in the strength of the correlations is that interannual variations in NPP, NMIN and EET associated with historical temperature and precipitation are less than spatial variations in NPP, NMIN and EET associated with contemporary, i.e., long term, temperature and precipitation.

3.6. Effects of clearing for cropland and urban areas

In the analyses above, we have addressed the response of potential terrestrial ecosystems to changing climate and atmospheric CO_2 concentration in order to establish a basic understanding of the processes controlling C storage in natural ecosystems. Land-use change in the past, however, has substantially modified land ecosystems in the conterminous US (Burke et al., 1995; Turner et al., 1995; also see Fig. 6). Based on the contemporary distribution of cropland and urban areas (Fig. 6), we estimate that natural ecosystems in the conterminous US lost a total of 17.7 Pg C as a result of cropland expansion and urbanization, including the loss of 12.9 Pg C of vegetation carbon and 4.8 Pg C of reactive soil organic carbon (Table 4). Almost 93% of the reduction in carbon storage was due to the clearing of natural ecosystems for cropland. The effect of urbanization on carbon storage was small.

If we assume that carbon does not accumulate in cropland and urban areas, net ecosystem production in the conterminous US in 1992–1993 is decreased by 69.0 Tg C yr^{-1} (Table 4). This means that the carbon storage capacity of contemporary ecosystems in the conterminous US is about half of that estimated for potential vegetation, 138.1 Tg C yr^{-1} for 1992–1993. Carbon storage

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Fig. 15. Biome-specific responses of net ecosystem production to a combination of historical CO_2 concentrations, air temperatures and precipitation in the conterminous US during the time period from 1900–1994. Heavy line shows 5-year running mean.
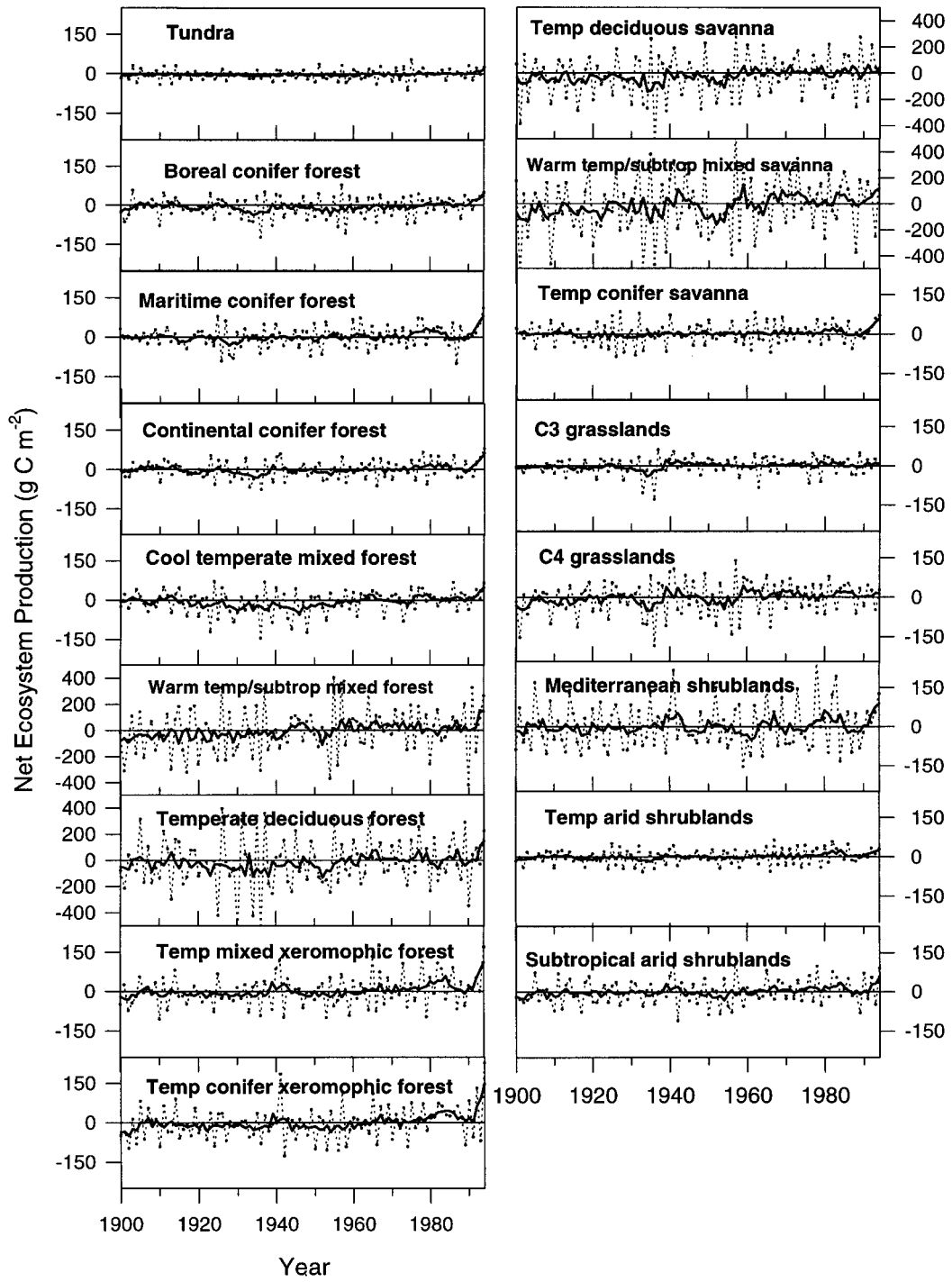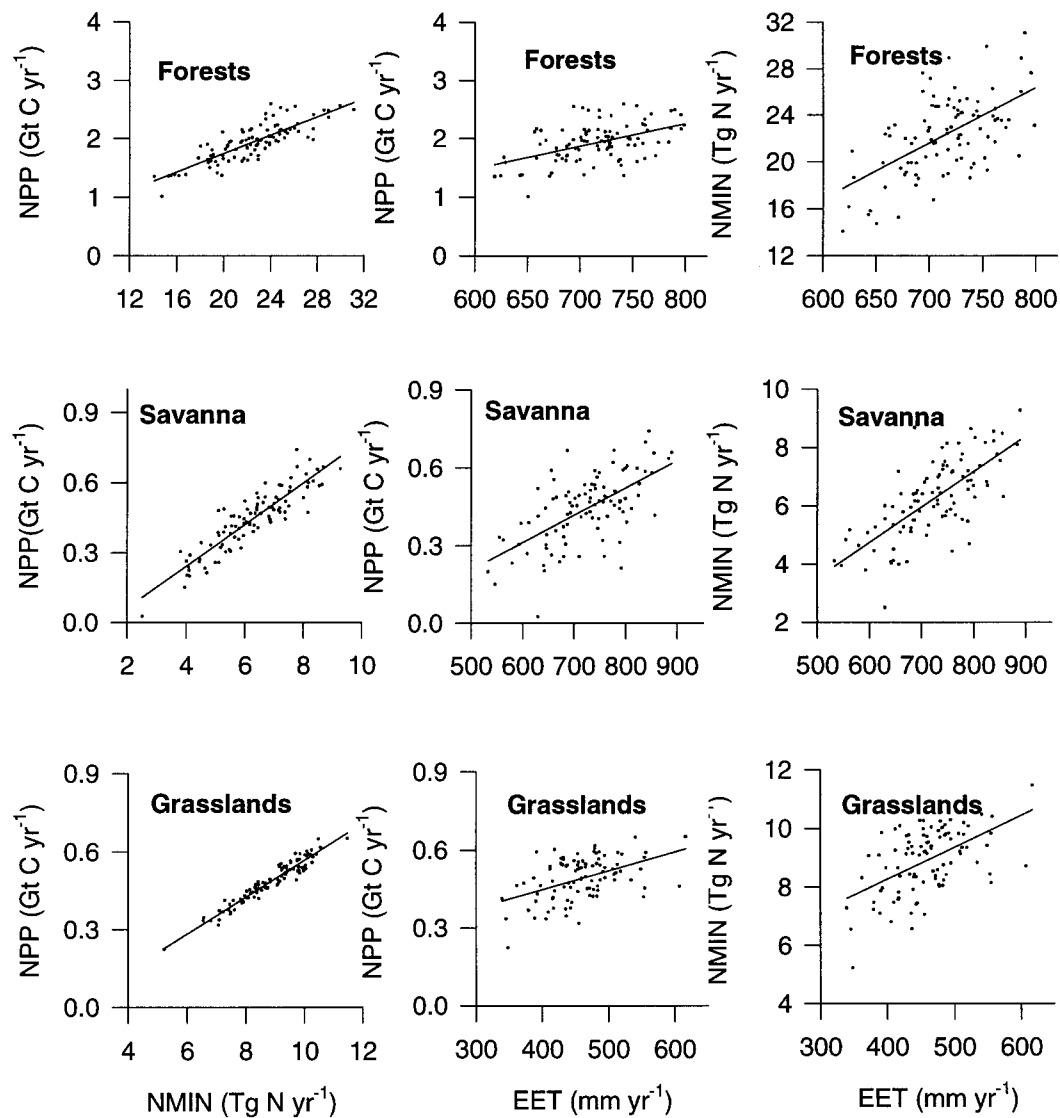
Fig. 16. Relationships among temporal changes in net primary production (NPP), net nitrogen mineralization (NMIN) and estimated evapotransporation (EET) for forest, savanna and grassland in response to a combination of historical CO_2 concentrations, air temperatures and precipitation in the conterminous US. Across: NPP versus NMIN: forests ($R = 0.83$, $P < 0.0001$), savanna ($R = 0.90$, $P < 0.05$), grasslands ($R = 0.96$, $P < 0.05$); NPP versus EET: forests ($R = 0.49$, $P < 0.0001$), savanna ($R = 0.62$, $P < 0.001$), grasslands ($R = 0.47$, $P < 0.0001$); and NMIN versus EET: forests ($R = 0.57$, $P < 0.0001$), savanna ($R = 0.71$, $P < 0.0001$), grasslands ($R = 0.52$, $P < 0.001$).

capacity in contemporary ecosystems, however, appears to have varied annually due to interannual climate varibility. The mean of net ecosystem production in contemporary ecosystems has been estimated to be 69 Tg C yr^{-1}, which is about 69% of net ecosystem production (100.1 Tg C yr^{-1}) for potential vegetation over the time period from 1980 to 1994.

Table 4. *Impact of natural ecosystem conversion on net ecosystem production, vegetation carbon, reactive soil organic carbon and total carbon storage in the conterminous US until the years 1992–1993*

	NEP[a] (Tg C yr^{-1})	VEGC[b] (Pg C)	SOILC[c] (Pg C)	TOTALC[d] (Pg C)
potential vegetation	138.1	55.9	41.3	97.2
actual vegetation	69.1	43.0	36.5	81.9
C loss due to cropland expansion*	65.5	12.0	4.5	16.5
C loss due to urbanization	3.5	0.9	0.3	1.2
decrease in carbon flux and storage	69.0	12.9	4.8	17.7

[a] NEP means net ecosystem production.
[b] VEGC means vegetation carbon.
[c] SOILC means reactive soil organic carbon.
[d] TOTALC means total carbon storage.

4. Discussion

4.1. Historical changes in terrestrial carbon storage

The estimates of TEM suggest that historical atmospheric CO_2 and climate variability between 1900–1994 caused a loss of 4.3 Pg C (4.2%) in the total carbon storage from potential vegetation in the conterminous US. This magnitude of simulated carbon loss in the conterminous US during the past century is closely associated with several periods of sustained low precipitation including the "Dust Bowl" in the 1930s. If correct, the loss of terrestrial carbon from natural ecosystems associated with climate variability over the past 95 years in the conterminous US has contributed to historical increases in atmospheric CO_2 concentration.

The TEM simulations also indicate that historical changes in temperature and precipitation have caused substantial interannual variability in the net exchange of carbon between terrestrial ecosystems and the atmosphere in the conterminous US. In years with low precipitation, terrestrial ecosystems tend to be carbon sources to the atmosphere. Interestingly, both the El Niño years of 1982/1983 and 1986/1987 and the La Niña year of 1988 exhibit dry growing season periods for much of the US. During El Niño and La Niña phases, the conterminous US appears to be a source of carbon to the atmosphere.

The TEM simulations lead us to suggest that natural terrestrial ecosystems have acted primarily as a sink of atmospheric CO_2 as a result of wetter weather and higher CO_2 concentrations in recent decades. This sink behavior is consistent with the recent measurements of latitudinal gradients of C^{13}–CO_2 (Ciais et al., 1995) and the ratio of O_2 to N_2 (Keeling et al., 1996) that suggest a Northern Hemisphere terrestrial sink. For the 1980s, our further analysis shows that the remaining natural terrestrial ecosystems of the conterminous US have accumulated 78.2 Tg C yr^{-1} because of the combined effect of increasing atmospheric CO_2 and climate variability. Natural forest ecosystems have accumulated 43 Tg C yr^{-1} for the same period, or 55% of the total carbon accumulation for the decade. During the 1980s, grasslands, shrublands and savannas accumulated 14.3 Tg C yr^{-1}, 12.0 Tg C yr^{-1}, and 8.9 Tg C yr^{-1}, which represent 18%, 15% and 11%, respectively, of the decadal carbon accumulation.

Recent reviews of the global carbon budget indicate that four factors can lead to increased carbon storage in terrestrial ecosystems: CO_2 fertilization, climate effect, nitrogen deposition and mid- and high-latitude forest regrowth following harvest (Schimel, 1995; Melillo et al., 1996). Turner et al. (1995) used forest inventory data to estimate that forests of the conterminous US accumulated 79 Tg C yr^{-1} during the 1980s. The forest inventory approach provides an estimate of carbon storage changes from all causes including forest growth responses to changes in climate and atmospheric CO_2, forest regrowth following disturbances, and forest growth responses to nitrogen deposition (Houghton, 1996). Our estimate of 43.0 Tg C yr^{-1} accumulated in forests in response to climate variability and increasing atmospheric CO_2 during the 1980s, which represents 54% of

the Turner et al.'s estimate of net carbon storage, suggests that ecosystem responses to changes in climate and CO_2 are a substantial component of historical changes in carbon storage. The role of changes in climate and CO_2 in the carbon budget, however, can vary annually due to interannual variability in climate and CO_2 growth rate. In the following sections, we further discuss the relationship of our results to the four factors: CO_2 fertilization, climate effect, nitrogen deposition and forest regrowth following harvest.

4.2. Effects of CO_2 fertilization on carbon storage

As the atmospheric concentration of CO_2 increases, plants may increase their uptake of carbon, which may increase terrestrial carbon storage. For the conterminous US, our simulations indicate that terrestrial responses to increasing atmospheric CO_2 during the past 95 years compensates for nearly half of the losses in carbon storage caused by climate variability alone. On the global scale, terrestrial ecosystem response to increasing atmospheric CO_2 accounts for a 0.5 to 2.0 Pg C yr^{-1} carbon sink during the 1980s (Melillo et al., 1996). Other studies also indicate that CO_2 fertilization represents an important part of carbon storage in terrestrial ecosystems (Gifford, 1993; Friedlingstein et al., 1995; Post et al., 1997; Kicklighter et al., 1999). The responses of TEM to increasing atmospheric CO_2 indicate that nitrogen availability represents a major constraint on the ability of terrestrial ecosystems to incorporate elevated CO_2 into production (McGuire et al., 1993, 1997; Melillo et al., 1993; Pan et al., 1998; Kicklighter et al., 1999). Relative responses tend to be greatest in dry ecosystems like arid shrublands which are more limited by water availability than by nitrogen availability (Melillo et al., 1993; Pan et al., 1998).

4.3. Effects of temperature and precipitation variability on carbon storage

The processes of photosynthesis and plant respiration have different sensitivities to temperature. For many mid-latitude plants, the response of photosynthesis to temperature is initially rapid above 0°C, but saturates over a wide range of temperatures. In contrast, plant respiration rates tend to be low below 20°C, but increase rapidly at higher temperatures. These differences in the sensitivity of photosynthesis and respiration to temperature have been used to support the argument that global warming may result in a reduction in net carbon uptake by plants (Woodwell, 1995).

For historical temperature variability in the conterminous US, increases in temperature are associated with simulated increases in primary production, decomposition, net nitrogen mineralization and evapotranspiration, but are associated with slight decreases in soil moisture. The high correlation between decomposition and temperature suggests that the temperature sensitivity of decomposition is stronger than the indirect effects of temperature on decomposition by decreasing soil moisture. Because the simulated changes in continental-scale soil moisture were very small, it is not clear if decomposition would be more sensitive to changes in soil moisture associated with larger temperature variability. In our simulations, production tends to increase with temperature because higher rates of decomposition enhance nitrogen availability through increased net nitrogen mineralization. Thus, in TEM, the temperature sensitivity of decomposition plays an important role in the response of plant production through the dynamics of the nitrogen cycle. Increases in nitrogen availability caused by warmer temperatures have also been shown in field experiments (Peterjohn et al., 1994, Melillo et al. 1995a) and other modeling studies (Schimel et al., 1996b). The consideration of carbon and nitrogen feedback will be a necessary component in assessments of carbon storage response to global warming.

Moisture availability influences production and decomposition in many ways (Melillo et al. 1990). Drought stress increases stomatal closure to decrease the internal concentration of CO_2 within leaves (Bazzaz, 1990; Mooney et al., 1991). Drought stress also influences the phenology of vegetation (Raich et al., 1991) to affect production. In addition, soil moisture influences decomposition, gross nitrogen mineralization, nitrogen immobilization, and nitrogen uptake by vegetation. For the historical period from 1900 to 1994, our simulations indicate that NPP was substantially more sensitive to precipitation variability than R_H. Although decreases in precipitation were tightly coupled to decreases in evapotranspiration and soil moisture, NPP was most sensitive to

changes in net nitrogen mineralization, and was more sensitive to changes in evapotranspiration than to changes in soil moisture. Our results also indicate that interannual variability in temperature and precipitation is relevant in assessments of carbon storage to projected climate change. In addition, in order to fully assess the effect of climate variability on carbon storage, we should take into account temporal variability in solar radiation. Data sets to do this kind of analysis are only now becoming available (Kittel et al., 1997).

4.4. Effects of nitrogen deposition on carbon storage

Nitrogen deposition from fertilizers and oxides of nitrogen released from the burning of fossil fuel during the 1980s is estimated to amount to a global total of 0.05–0.08 Pg N yr^{-1} (Melillo et al., 1996). Forests in eastern North America receive up to 17 kg N ha^{-1} yr^{-1} (Melillo et al., 1989). Many terrestrial ecosystems in middle and high latitudes are nitrogen limited (Melillo and Gosz, 1983; Vitousek and Howarth, 1991, Melillo et al., 1995b; Schimel, 1995). In general, nitrogen inputs should enhance terrestrial carbon storage (Melillo and Gosz, 1983; Schindler and Bayley, 1993; Hudson et al., 1994; Schimel et al., 1994; Galloway et al., 1995; Townsend et al., 1996; Holland et al., 1997), but it is also possible that chronic high inputs of nitrogen may cause terrestrial ecosystems to lose carbon (Aber et al., 1993). To assess the effects of nitrogen deposition in a geographically specific manner, large-scale ecological models require spatially explicit data sets of nitrogen deposition. Several efforts are attempting to develop spatially explicit data sets of nitrogen deposition for the ecological modeling community (Holland et al., 1997). As a database containing a time series of nitrogen deposition was not available for our transient analyses, we ran the model with a closed nitrogen cycle; that is, we did not attempt to estimate the effects of nitrogen deposition on carbon storage in this analysis. This can bias the estimates of carbon storage either high or low depending on the nature of the interannual climate variations.

4.5. Effect of land-use change on carbon storage

Our analyses have shown that the conversion of natural ecosystems to cropland and urban areas can release substantial amounts of carbon to the atmosphere through the loss of carbon from both vegetation and soils. For the conterminous US during the period from 1980 to 1994, we estimate that the historical conversion of natural ecosystems to cropland and urban areas could cause a 31% of reduction in net ecosystem production. We have estimated that natural ecosystems in the conterminous US lost a total of 17.7 Pg C as a result of cropland expansion and urbanization since settlement times. The TEM analysis shows that climate variability, coupled with increased atmospheric CO_2, caused a 4.3 Pg C decrease in the conterminous US over the 95 years. Our analysis indicates that land-use change has been a major factor in determining carbon storage in the conterminous US. However, this first order analysis does not evaluate how changes in vegetation structure associated with changes in land use and agricultural intensification have affected carbon dynamics of terrestrial ecosystems in the conterminous US.

The fate of cleared lands is another factor that affects carbon fluxes and storage (Melillo et al., 1988; Dixon et al., 1994; Hall et al., 1995; Kurz and Apps, 1995; Tian et al., 1995; Turner et al., 1995; Brown et al., 1996; Houghton, 1996). Many forests and woodlands in the northeast of the US had been converted to croplands and pastures in the last century, but those croplands and pastures have been abandoned and returned to forests since the early part of this century (Foster, 1992). Terrestrial ecosystems following disturbances may be in various stages of succession. This complexity in the path and direction of vegetation succession following human and natural disturbances (Bormann and Likens, 1979; Pickett and White, 1985; Tian and Qi, 1990) may also interact with changes in atmospheric CO_2 and climate variability to influence the temporal dynamics of carbon fluxes and pool sizes (Pastor and Post, 1986; Solomon, 1986; Smith and Shugart, 1993). Thus, to improve our understanding of terrestrial carbon dynamics in response to changing climate and atmospheric chemistry, changes in vegetation structure must be incorporated into a framework of transient ecosystem dynamics (Smith and Shugart, 1993, Woodward et al., 1995, Pitelka et al., 1997, Tian et al., 1998b).

4.6. The validation and verification of the model

In our earlier work with TEM we have attempted to check the model results against several types of

field measurements. One of our approaches has
been to check TEM output against field-derived
NPP measured across the globe. We found the
comparisons to be reasonable (Raich et al., 1991;
McGuire et al., 1992; Melillo et al., 1993). Another
approach has been to check NEP derived from
TEM against NEP estimates based on measure-
ments made with the eddy covariance technique.
We recently did this for three sites in the Amazon
Basin and found that the TEM estimates for NEP
for two tropical forest sites and one savanna site
were close to the measurements (Tian et al., 1998a).

The TEM model was originally developed by
us using much of the carbon and nitrogen cycling
data available for ecosystems in the US. For
example, the Harvard Forest data on NPP and
NEP measured by the eddy covariance technique
have been used in our model development efforts.
We need new data to check how well TEM
performs for ecosystems in the US.

In our opinion, some of the best data for
checking TEM will come from long-term eddy
covariance studies. We are therefore particularly
supportive of new Ameriflux long-term network
that will conduct long-term eddy covariance stud-
ies across gradients within biomes in North
America.

5. Conclusions

We have explored how climate variability and
increasing atmospheric CO_2 concentration in the
past century may have affected the carbon fluxes
and storage of terrestrial ecosystems in the conter-
minous US. Our results show that net carbon
exchange between the atmosphere and the terrest-
rial ecosystems of the conterminous US exhibits
substantial year-to-year variability. This variabil-
ity in net carbon storage is primarily related to
the sensitivity of NPP to the interannual variabil-
ity in precipitation. Thus, regional estimates of net
carbon exchange based on single year measure-
ments must be viewed cautiously.

Our results also indicate that net carbon
exchange between the atmosphere and terrestrial
ecosystems in the conterminous US exhibits deca-
dal variations. At a century time scale, the poten-
tial terrestrial ecosystems in the conterminous US
acted as a source of atmospheric CO_2 primarily
due to drought stress. However, these terrestrial

ecosystems have acted primarily as a sink of
atmospheric CO_2 for the past three decades.

The conversion of some of the nation's natural
ecosystems to croplands and urban areas has
reduced the year-to-year capacity of land eco-
systems to store carbon. For the fifteen years from
1980 to 1994, the average annual reduction was
31% (31 Tg). In addition to considering land use,
a detailed assessment of the capability of terrestrial
ecosystems to sequester atmospheric CO_2 needs
to account for various aspects of CO_2 fertilization,
climate, nitrogen deposition and forest regrowth.

6. Acknowledgments

7. Appendix

Carbon exchange between terrestrial ecosystems
and the atmosphere depends on gross primary
production (GPP), autotrophic respiration (R_A),
and heterotrophic respiration (R_H). Here, we pro-
vide additional details of the algorithms and feed-
backs associated with GPP, R_A, and R_H that are
influenced by changes in atmospheric CO_2, tem-
perature, and precipitation. We also provide
details of model modifications that were incorpor-
ated in version 4.1 of TEM.

7.1. Gross primary production

The flux GPP considers the effects of several
factors and is calculated at each monthly time
step as follows:

$$GPP = C_{max} f(PAR) f(LEAF) f(T) f(C_a, G_v) f(NA),$$

where C_{max} is the maximum rate of C assimilation,

PAR is photosynthetically active radiation, LEAF is leaf area relative to maximum annual leaf area (phenology), T is temperature, C_a is atmospheric CO_2 concentration, G_v is relative canopy conductance, and NA is nitrogen availability. Nitrogen availability also influences the ability of vegetation to incorporate elevated CO_2 into production (Pan et al., 1997; McGuire et al., 1997). In version 4.1 of TEM, elevated atmospheric CO_2 decreases the nitrogen concentration of vegetation to influence both nitrogen requirement of production and decomposition (McGuire et al., 1997). Temperature directly influences $f(T)$, indirectly influences $f(\text{LEAF})$ and $f(C_a, G_V)$ through effects on estimated evapotranspiration as well as potential evapotranspiration, and indirectly influences nitrogen availability through effects on the rates of nitrogen uptake, decomposition, and net nitrogen mineralization. Precipitation influences $f(\text{LEAF})$ and $f(C_a, G_V)$ through effects on estimated evapotranspiration and influences nitrogen availability through soil moisture effects on the rates of nitrogen uptake, decomposition, and net nitrogen mineralization.

The effects of elevated atmospheric CO_2 directly affect GPP altering intercellular CO_2 in $f(C_a, G_V)$. Temperature also influences this function by effects on potential evapotranspiration (PET), and both temperature and precipitation influence this function by effects on estimated evapotranspiration (EET). The response of GPP to atmospheric CO_2 is affected by three aspects of leaf-level carbon assimilation: carboxylation, light harvest and carbohydrate synthesis (Farquhar et al., 1980; Wullschleger, 1993; Pettersson and McDonald, 1994; Sage, 1994). The assimilation–intercellular CO_2 (A–C_i) relationship is the empirical observation of carboxylation-limited, light-limited, and synthesis-limited assimilation over the range of intercellular CO_2 (Wullschleger, 1993; Sage, 1994). In TEM, the A-C_i relationship is modeled with a hyperbolic relationship that collectively represents the mechanisms of carbon assimilation in the function $f(C_a, G_V)$:

$$f(C_a, G_v) = C_i/(k_c + C_i),$$

where C_i is the concentration of CO_2 within leaves of the canopy and k_c is the half-saturation constant for CO_2 uptake by plants. The variable C_i is the product of ambient CO_2 (C_a) and relative canopy conductance to CO_2 (G_v), a variable which increases from 0–1 with increasing water availability and depends on the ratio of EET to PET:

$$G_v = -10\,(\text{EET}/\text{PET})^2 \qquad \text{EET}/\text{PET} \leqslant 0.1$$
$$+ 2.9(\text{EET}/\text{PET})$$

$$G_v = 0.1 + 0.9\,(\text{EET}/\text{PET}) \qquad \text{EET}/\text{PET} > 0.1.$$

The different form of G_v below an EET/PET of 0.1 allows G_V to be 0.0 in extremely arid regions. Because G_V depends on the ratio of EET to PET, the response of $f(C_a, G_v)$ to doubled CO_2 is higher in dry environments (Melillo et al., 1993; Pan et al., 1997). Decreasing moisture availability is assumed to increase stomatal closure, thereby decreasing the internal CO_2 concentration. This relationship is based on the tight correlation found between transpiration rates and CO_2 assimilation (Chang, 1969; Kramer, 1983). The value of the parameter k_c, 400 ppmv, has been chosen to increase $f(C_a, G_v)$ by 37% for a doubling of atmospheric CO_2 from 340 ppmv to 680 ppmv for maximum relative canopy conductance, that is, $G_v = 1$ (McGuire et al., 1992, 1993, 1997).

Temperature and precipitation influences $f(\text{LEAF})$ through effects on EET. In TEM, water availability influences the phenology of vegetation through $f(\text{LEAF})$ as follows:

$$\text{LEAF}_j = a(\text{EET}_j/\text{EET}_{\max}) + b(\text{LEAF}_{j-1}) + c,$$

$$\text{LEAF}_j = 1.0 \qquad \text{if } \text{LEAF}_j > 1.0$$

$$\text{LEAF}_j = \text{LEAF}_i/\text{LEAF}_{\max} \qquad \text{if } \text{LEAF}_{\max} < 1.0$$

$$\text{LEAF}_j = \min \qquad \text{if } \text{LEAF}_j < \min,$$

where $\text{EET}_{\max}$ is the maximum EET occurring during any month j; a, b and c are regression-derived parameters; min is the minimum value of relative photosynthetic capacity for a biome and $\text{LEAF}_{\max}$ refers to the maximum predicted LEAF for a specific location (Raich et al., 1991).

Temperature also influences GPP through effects of the function $f(T)$:

$$f(T) = 0 \qquad T < T_{\min} \text{ or } T > T_{\max}$$

$$f(T) = \frac{(T - T_{\min})(T - T_{\max})}{[(T - T_{\min})(T - T_{\max})]} \qquad T_{\min} \leqslant T < T_{\text{opt mim}}$$
$$- (T - T_{\text{opt min}})2$$

$$f(T) = 1 \qquad T_{\text{opt mim}} \leqslant T < T_{\text{opt max}}$$

$$f(T) = \frac{(T - T_{\min})(T - T_{\max})}{[(T - T_{\min})(T - T_{\max})]} \qquad T_{\text{opt max}} \leqslant T \leqslant T_{\max},$$
$$- (T - T_{\text{opt max}})2$$

where T is the mean monthly air temperature
(°C), T_{min} and T_{max} are the maximum and
minimum constraints for GPP, and T_{optmin} and
T_{optmax} represent the range of temperature for
optimal carbon uptake. The values of T_{min} and
T_{max} are set so that they represent the monthly
growing-season limits of the vegetation type. To
allow for local temperature adaptation/
acclimation, T_{optmin} is defined by the mean
monthly air temperature that corresponds to the
month of maximum leaf area. The temperature
T_{optmax} is generally set to be approximately 1°C
less than T_{max}.

Changes in atmospheric CO_2, temperature,
and precipitation influence nitrogen availability
in a number of ways. In version 4.1 of TEM,
elevated atmospheric CO_2 also decreases the
nitrogen concentration of vegetation to influence
both nitrogen requirement of production and
decomposition. Temperature influences nitrogen
availability through effects on the temperature-
sensitive rates of nitrogen uptake, decomposi-
tion, and net nitrogen mineralization. Both
temperature and precipitation influence nitrogen
availability through soil moisture effects on the
rates of nitrogen uptake, decomposition, and net
nitrogen mineralization. The degree to which
these effects on nitrogen availability influence
GPP depends on the carbon–nitrogen status of
the vegetation.

In TEM, the carbon–nitrogen status of the
vegetation influences the calculation of GPP
through the feedback of nitrogen availability on
carbon assimilation. This feedback, which is rep-
resented by $f(NA)$, is determined by the status of
nitrogen supply which is the sum of nitrogen
uptake (NUPTAKE) plus nitrogen mobilized from
the vegetation labile nitrogen pool (NMOBIL).
The feedback represented by $f(NA)$ is dynamically
determined by comparing the calculation of GPP
based on nitrogen supply and the calculation of
GPP for no constraints of nitrogen supply (GPP_P)
as follows:

$$\begin{cases} NPP = Pcn\,(NUPTAKE + NMOBIL) \\ GPP = Pcn\,(NUPTAKE + NMOBIL) + R_A \\ f(NA) = GPP/GPP_p \\ \text{when } Pcn\,(NUPTAKE + NMOBIL) \\ \qquad + R_A < GPP_p \end{cases}$$

and

$$\begin{cases} NPP = GPP_p - R_A \\ GPP = GPP_p \\ f(NA) = 1 \\ \text{when } Pcn\,(NUPTAKE) + NMOBIL) \\ \qquad + R_A \geqslant GPP_p, \end{cases}$$

where Pcn is the C to N ratio of production,
NUPTAKE is nitrogen uptake, NMOBIL is nitro-
gen mobilized from the vegetation labile nitrogen
pool, and R_A is autotrophic respiration.

On first inspection, these algorithms would
appear to completely constrain the response of
NPP to elevated CO_2 in nitrogen limited systems.
However, it is important to recognize that there
is seasonality in the degree of nitrogen limitation.
Nitrogen is generally in greatest supply early in
the growing season when vegetation is able to
mobilize nitrogen from storage. In this case, the
vegetation in TEM is able to incorporate elevated
intercellular CO_2 into production. Higher levels
of production cause greater litterfall to cause
higher rates of decompostion and higher rates of
nitrogen cycling. One consequence of greater
nitrogen cycling is higher rates of nitrogen uptake.
Thus, elevated CO_2 alters the seasonal pattern of
carbon–nitrogen status in the vegetation of TEM
to influence production.

Elevated CO_2 also influences carbon–nitrogen
status of the vegetation by altering the nitrogen
concentration of vegetation (McGuire et al., 1995,
1997). Experimental studies that have measured
the response of tissue nitrogen concentration in
plants exposed to elevated CO_2 usually do not
identify whether the measurements represent
changes in new production or overall vegetation
biomass. Therefore, we altered the parameters in
TEM that control vegetation carbon to nitrogen
ratio (Vcn; see Raich et al. (1991)) and the produc-
tion carbon to nitrogen ratio (Pcn, see McGuire
et al. (1992)). We make the assumption of a linear
15% decrease in nitrogen concentration associated
with a 340 ppmv increase in atmospheric CO_2
(McGuire et al., 1995, 1997). Because nitrogen
concentration is inversely related to carbon to
nitrogen ratio, we modified Vcn and Pcn as fol-
lows:

$$Vcn(dC_a)) = Vcno(1.0 + [dC_a\;dVcn])$$

and

$$\text{Pcn}(dC_a) = \text{Pcno}(1.0 + [dC_a\,d\text{Pcn}]),$$

where Vcno and Pcno are the original values of Vcn and Pcn, and $\text{Vcn}(dC_a)$ and $\text{Pcn}(dC_a)$ are the values of Vcn and Pcn associated with the increase in atmospheric CO_2, dC_a, and with the per-ppmv changes in carbon to nitrogen ratios, dVcn and dPcn. The per-ppmv changes in carbon to nitrogen ratio are calculated as follows:

$$d\text{Vcn} = ([100/(100 - d[N])] - 1.0)/340$$

and

$$d\text{Pcn} = ([100/(100 - d[N])] - 1.0)/340,$$

where $d[N]$ is the assumed percent decrease in nitrogen concentration associated with a 340 ppmv increase in the concentration of atmospheric CO_2.

7.2. Autotrophic respiration

In TEM, the flux R_A represents total respiration (excluding photorespiration) of living vegetation, including all CO_2 production from the various processes of plant respiration, nutrient uptake, and biomass construction. In TEM, R_A is the sum of growth respiration, R_g, and maintenance respiration, R_m. Growth respiration is estimated to be 20% of the difference between GPP and maintenance respiration (Raich et al., 1991). Changes in atmospheric CO_2, temperature, and moisture influence growth respiration through effects on GPP. Temperature also influences growth respiration through effects on maintenance respiration. We model maintenance respiration as a direct function of plant biomass (C_V) as follows:

$$R_m = K_r(C_V)\,e^{rT},$$

where K_r is the per-gram-biomass respiration rate of the vegetation at $0°C$, C_V is the mass of carbon in the vegetation, T is mean monthly air temperature, and r is the instantaneous rate of change in respiration with change in temperature. The parameter r depends on temperature and is calculated as described in McGuire et al. (1992). In version 4.1 of TEM we added an algorithm that alters the parameter K_r to represent the accumulation of tissues with low metabolic rate such as heartwood in woody vegetation and structural carbon in non-woody vegetation.

In earlier versions of TEM, K_r is a constant over the entire range of vegetation carbon within a vegetation type. In forest stands, K_r should decrease after canopy closure because of the accumulation of heartwood volume, which has a low metabolic rate, after sapwood volume saturates. Similarly, in herbaceous vegetation the accumulation of more structural material with higher biomass should cause K_r to decrease. When we plotted K_r values of woody vegetation types in the calibration data set of version 4.0, we found a negative linear relationship between the natural logarithm of K_r and C_V such that:

$$\ln(K_r) = K_{ra}C_V + K_{rb},$$

where K_{ra} is the slope and K_{rb} is the intercept of the relationship. We implemented this relationship in version 4.1 of TEM and recalculated K_{rb} for each vegetation type by forcing the relationship through the version 4.0 K_r value of the vegetation type. For non-woody vegetation types, we regressed the $\ln(K_r)$ against C_V to determine K_{ra} and then determined K_{rb} for each vegetation type by forcing the relationship through the version 4.0 K_r value of the vegetation type.

7.3. Heterotrophic respiration

In TEM, decomposition is represented as heterotrophic respiration (R_H):

$$R_H = K_d C_S f(M_V)\,e^{0.0693T},$$

where K_d is the heterotrophic respiration rate at $0°C$, C_S is carbon storage in soils, $f(M_V)$ is a function defining the influence of volumetric soil moisture on decomposition, and T is mean monthly air temperature. In TEM, R_H is the only loss calculated from the detrital compartment C_S, which is an aggregated pool of organic carbon in detritus and soils. In version 4.1, changes in atmospheric CO_2 influence the parameter K_d, which is sensitive to increases in the carbon to nitrogen ratio of litterfall that are associated with elevated atmospheric CO_2 (McGuire et al., 1997). Temperature directly influences R_H directly through effects on $e^{0.0693T}$. Both temperature and precipitation influence soil moisture to affect $f(M_V)$. Changes in CO_2 concentration, temperature, and precipitation also influence R_H through effects on NPP that affect the pool size of soil organic matter through changes in litterfall input.

The parameter K_d, which represents the heterotrophic respiration rate at 0°C, is the rate-limiting parameter in the R_H formulation. The value K_d at a vegetation-specific calibration site is K_{dc}, which is one of several rate-limiting parameters that are determined by calibrating TEM to the annual fluxes and pools at the calibration site for an ecosystem. K_{dc} depends on soil texture according the relationship:

$$K_{dc} = K_{dca}/P_{SC} + K_{dcb},$$

where P_{SC} is the proportion of silt plus clay and K_{dca} and K_{dcb} are empirically determined parameters that describe the inverse relationship between K_{dc} and P_{SC}. The inverse relationship represents the physical protection of soil organic matter in fine-textured soils. To implement changes in litter quality associated with changes in vegetation nitrogen concentration, we relate K_d to a power function of the carbon to nitrogen ratio of litterfall:

$$K_d = K_{dc}(L_C/L_N)^{-0.784}/(L_{Cc}/L_{Nc})^{-0.784},$$

where L_C and L_N are the annual fluxes of litterfall carbon and nitrogen and where L_{Cc} and L_{Nc} are the annual fluxes of litterfall carbon and nitrogen at the calibration site for the ecosystem. The implementation of this power function is based on the relationship derived by Melillo et al. (1982) for the decomposition of 13 leaf and needle species in the laboratory study of Daubenmire and Prusso (1963). The relationship identifies that an inverse curvilinear relationship exists between the rate constant for annual mass loss, k (Jenny et al., 1949), and the initial lignin to nitrogen ratio according to a power function with the exponent -0.784. We used this relationship instead of other relationships (Melillo et al., 1982) because the data used to derive the relationship represents a wider range of lignin to nitrogen ratios than data

used to derive other relationships; in TEM, the aggregated nature of litter inputs into the soil requires a relationship appropriate to a broad gradient of litter quality. Our implementation of this relationship to determine the dependence of K_d on litter quality assumes that K_d is proportional to k (Raich et al., 1991) and that the ratio of k to (lignin/nitrogen)$^{-0.784}$ is a constant (Melillo et al., 1982). Finally, we use the carbon to nitrogen ratio of litterfall in place of the initial lignin to nitrogen ratio of litterfall. The sensitivity of the estimates of NPP and carbon storage by TEM for our implementation of the new K_d algorithm to changes in vegetation nitrogen concentration associated with elevated CO_2 have been evaluated by McGuire et al. (1997).

The function $f(M_V)$ is a nonlinear relationship that models the influence of volumetric soil moisture on microbial activity at low soil-moisture contents and the influence of oxygen availability on microbial activity at high moisture contents:

$$f(M_V) = \frac{(M_V - M_{Vmin})(M_V - M_{Vmax})}{[(M_V - M_{Vmin})(M_V - M_{Vmax})]} ,$$
$$- (M_V - M_{Vopt})^2$$

where M_{Vmin} (0%), M_{Vopt} (50%), and M_{Vmax} (100%) are the minimum, optimum, and maximum volumetric soil moistures for decomposition. This relationship causes the highest rate of decomposition when soils are 50% water by volume.

The exponential relationship with T represents the temperature sensitivity of decomposition, which increases logarithmically with a Q_{10} of 2.0 over all temperatures; soil respiration in temperate forest soils has a Q_{10} of 1.988 in relationships with mean daily air temperature and 1.983 in relationships with mean monthly air temperature (Kicklighter et al., 1994).

REFERENCES

Aber, J. D., Magill, A., Boone, R., Melillo, J. M., Steudler, P. A. and Bowden, R. 1993. Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. *Ecol. Appl.* **3**, 156–166.

Aber, J. D. and Driscoll, C. T. 1997. Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests. Glob. Biogeochem. Cyc. **11**, 639–648.

Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO_2 levels. *Anna. Rev. Ecol. Syst.* **21**, 167–176.

Bormann, F. H. and Likens, G. E. 1979. *Pattern and process in a forested ecosystem.* Springer-Verlag, New York.

Brown, S. A., Sathaye, J., Cannell, M. and Kauppi, P. 1996. Management of Forests for Mitigation of Green-

house gas emissions. In: *IPCC climate change 1995* (eds. R.T. Watson, M.C. Zinyowera and R.H. Moss). Cambridge University Press, pp. 773–797.

Burke, I. C., Lauenroth, W. K. and Coffin, D. P. 1995. Soil organic matter recovery in semiarid grasslands: Implications for the conservation reserve program. *Ecol. Appl.* **5**, 793–801.

Braswell, B. H., Schimel, D. S., Linder, E. and Moore III, B. 1997. The response of global terrestrial ecosystems to interannual temperature variability. *Science* **278**, 870–872.

Chang, J.-H. 1968. *Climate and agriculture: an ecological survey.* Aldine, Chicago, Illinois, USA.

Ciais, P., Tans, P., Trolier, M., White, J. and Francey, R. 1995. A large northern hemisphere terrestrial CO_2 sink indicated by $^{13}C/^{12}C$ of atmospheric CO_2. *Science* **269**, 1098–1102.

Dai, A., and Fung, I. 1993. Can climate variability contribute to the "missing" CO_2 sink? *Glob. Biogeochem. Cyc.* **7**, 599–609.

Daly C, Neilson, R. and Philips, D. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *J. of Applied Meteorology* **33**, 140–158.

Dixon, R., Brown, S., Houghton, R., Solomon, A., Trexler, M. and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**, 185–190.

Ehleringer, J. and Field, C. 1993. *Scaling physiological processes: leaf to globe.* Academic Press, Inc. San Diego.

Enting, I., Wigley, T. and Heimann, M. 1994. Future emissions and concentrations of carbon dioxide: key ocean/atmosphere/land analyses. *CSIRO Division of Atmospheric Research Technical Paper no.* **31**, 120 pp.

Foster, D. R. 1985. Vegetation development following fire in Picea Mariana (black spruce)-Pleurozium forests of south-eastern Labrador, Canada. *J. Ecology* **73**, 517–534.

Foster, D. R. 1992. Land use history (1730–1990) and vegetation dynamics in central New England, USA. *J. of Ecology* **80**, 753–772.

Friedlingstein, P., Fung, I., Holland, E., John, J., Brasseur, G., Erickson, D. and Schimel, D. 1995. On the contributionof the biosphere CO_2 fertilization to the missing sink. *Glob. Biogeochem.* Cycle **9**, 541–556.

Galloway, J., Schlesinger, W., Levy II, H., Michaels, A. and Schnoor, J. 1995. Nitrogen fixation: Anthropogenic enhancement environmental response. *Glob. Biogeochem. Cyc.* **9**, 235–252.

Gifford, R. M. 1993. Implications of CO_2 effects on vegetation for the global carbon budget. In: *The global carbon cycle* (ed. M. Heimann), Proceedings of the NATO Advanced Study Institute, Il Ciocco, Italy, 8–20 September 1991, pp. 165–205.

Glassy, J. and Running, S. 1994. Validating diurnal climatology logic of MT-CLIM model across a climate gradient in Oregon. *Ecol. Appl.* **4**, 248–257.

Goulden, M., Munger, J., Fan, S., Daube, B. and Wofsy, S.

1996. Exchange of carbon dioxide by a deciduous forest response to interannual climate variability. *Science* **271**, 1576–1578.

Grace, J., Lloyd, J., McIntyre, J., Miranda, A., Meri, P., Miranda, H., Nobre, C., Monteith, J. Massheder, J., Wright, I. and Gash, J. 1995. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993. *Science* **270**, 778–780.

Hall, C., Tian, H., Qi, Y., Pontius, G. and Cornell, J. 1995. Modeling spatial and temporal pattern of tropical land use change. *J. of Biogeography* **22**, 753–757.

Hall, C., Tian, H. and Qi, Y. 1993. Responses of the biosphere to changing global environments: Evidence from the historic record of global biometabolism. *World Resource Rev.* **5**, 207–213.

Heimann, M., et al. 1997a. Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO_2: First results of a model intercomparison study. *Glob. Biogeochem. Cyc.* **12**, 10–24.

Heimann, M., et al. 1997b. Interannual variability of CO_2 exchange fluxes as simulated by four terrestrial biogeochemical models. In: *The extended abstract of the 5th International Carbon dioxide Conference* (eds. Ruth Baum et al.). Cairns, Australia, pp. 129–130.

Holland, E., Braswell, B., Lamarque, J-F, Townsend, A. et al. 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems, *J. Geophys. Res.* **102**(D13), 15849–15866.

Houghton, R. A. 1995. Effects of land-use change, surface temperature, and CO_2 concentration on terrestrial stores of carbon. In: *Biotic feedbacks in the global climatic system* (eds. G. M. Woodwell and F. T. Mackenzie). Oxford University Press, New York, pp. 333–366.

Houghton, R. A. 1996. Terrestrial sources and sinks of carbon inferred from terrestrial data. *Tellus* **48B**, 420–432.

Hudson, R., Gherini, S. and Goldstein, R. 1994. Modeling the global carbon cycle: Nitrogen fertilization of the terrestrial biosphere and the "missing" CO_2 sink. *Glob. Biogeochem. Cyc.* **8**, 307–333.

Hulme, M. 1995. *A historical monthly precipitation data for global land areas from 1900 to 1994, gridded at 3.75×2.5 resolution.* Constructed at climate research unit, University of East Anglia, Norwich, UK.

Hunt, E., Piper, S., Nemani, R., Keeling, C., Otto, R. and Running, S. 1996. Global net carbon exchange and intra-annual atmospheric CO2 concentration predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Glob. Biogeochem. Cyc.* **10**, 431–456.

Jenny, H., Gessell, S. and Bingham, S. 1949. Comparative study on decomposition rates of organic matter in temperate and tropical regions, *Soil Sci.* **68**, 419–432.

Jones, P. D. 1994. Hemispheric surface air temperature variations: a reanalysis and an update to 1993. *J. Clim.* **7**, 1794–1802.

Kaduk, J.and Heimann, M. 1994. The climate sensitivity of the Osnabruck biosphere model on the ENSO time scale. *Ecol. Model.* **75/76**, 239–256.

Karl, T., Easterling, D., Knight, R. and Hughes, P. 1994. U.S. national and regional temperature anomalies. pp.686–736. In: *Trends'93: a compendium of data on global change* (eds. T. A. Boden, D. P. Kaiser, R. J. Sepanski and F. W. Stoss). ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tenn., USA.

Keeling, C. D., Chin, J. and Whorf, T. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature* **382**, 146–149.

Keeling, R. F., Piper, S. and Heimann, M. 1996. Global and hemispheric CO_2 sinks deduced from changes in atmospheric O_2 concentration. *Nature* **381**, 218–221.

Kern, S. J. 1995. Spatial patterns of soil organic carbon in contiguous US. *Soil Sci. Soc. Amer. J.* **58**, 439–455.

Kicklighter, D., Melillo, J., Peterjohn, W., Rastetter, E., McGuire, A. and Steudler, P. 1994. Aspects of spatial and temporal aggregation in estimating regional carbon dioxide fluxes from temperate forest soils. *J. Geophys. Res.* **99**, 1303–1315.

Kicklighter, D.W. et al. 1999. A first order analysis of the potential role of CO_2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus* **51B**, 343–366.

Kindermann J., Wurth, G., Kohmaier, G. and Badeck, F-W. 1996. Interannual variation of carbon exchange fluxes in terrestrial ecosystems. *Glob. Biogeochem. Cyc.* **10**, 737–755.

King, A. W., W. M. Post and S.D. Wullschleger. 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO_2. *Climatic Change* **35**, 199–227.

Kittel, T., Rosenbloom, N., Painter, T., Schimel, D. and VEMAP Participants. 1995. The VEMAP integrated database for modeling United States ecosystem/vegetation sensitivity to climate change. *J. of Biogeography* **22**, 857–862.

Kittel, T. G. F. et al. 1997. A gridded historical (1895–1993) bioclimate dataset for the conterminous US. *Proceedings of the 10th Conference on Applied Climatology*, Boston, pp. 222–229.

Kramer, P. J. 1983. *Water relations of plants.* Academic Press, New York, USA.

Kuchler, A. W. 1964. *Manual to accompany the map, potential natural vegetation of the conterminous US.* Special Publication, No.**36**, American Geographical Society, New York, 143 pp.

Kuchler, A. W. 1975. *Potential natural vegetation of the US*, 2nd edition (map 1 :3,168,000). American Geographical Society, New York.

Kurz, W. A. and Apps, M. J. 1996. Retrospective assessment of carbon flows in Canadian boreal forests. In: *Forest ecosystems, forest management and the global carbon cycle* (eds. M. J. Apps and D. T. Price). NATO ASI Series 1: Global Environmental Change, Springer-Verlag, Heidelberg, Vol. 40, pp. 173–182.

Leemans, R. and Cramer, W. *The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid.* International Institute for Applied Systems Analysis (IIASA). RR-91–18.

Lieth, H. 1975. Modelling the primary productivity of the world, In: *Primary productivity of the biosphere* (eds. H. Lieth and R. H. Whittaker). Springer-Verlag, New York, pp. 237–263.

Loveland, T. R. and A. S. Belward, 1997. The IGBP-DIS global 1 km land-cover data set, DISCOVER-first results. *Int. J. Remote Sensing* **18**, 3291–3295.

Marks, D. 1990. The sensitivity of potential evapotranspiration to climate change over the continental United States. In: *Biospheric feedback to climate change: the sensitivity of regional trace gas emissions, evapotranspiration, and energy balance to vegetation redistribution* (eds. Gucinski, H., Marks, D. and Tuner, D. P.). EPA/600/3–90/07.S. Environmental Protection Agency, Corvallis, IV-1–IV-31.

Marland, G., Boden, T., Griffin, R., Huang, S., Kanciruk, P. and Nelson, T. 1989. *Estimates of CO_2 emissions from fossil fuel burning and cement manufacturing using the UN energy statistics and the US Bureau of Mines cement manufacturing data.* Oak Ridge Natl. Lab. Rep., ORNL/CDIAC 25.

McGuire, A. D., Melillo, J., Joyce, L., Kicklighter, D., Grace, A., Moore III, B. and Vorosmarty, C. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Glob. Biogeochem. Cyc.* **6**, 101–124.

McGuire, A. D., Joyce, L., Kicklighter, D., Melillo, J., Esser, G. and Vorosmarty, C. 1993. Productivity response of climax temperate forests to elevated temperature and carbon dioxide: a North American comparison between two global models. *Clim. Change* **24**, 287–310.

McGuire, A. D., Melillo, J., Kicklighter, D. and Joyce, L. 1995. Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates. *J. of Biogeography* **22**, 785–796.

McGuire, A. D., Melillo, J., Kicklighter, D., Pan, Y., Xiao, X., Helfrich, J., Moore III, B., Vorosmarty, C. and Schloss, A. 1997. Equilibrium response of global primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. *Glob. Biogeochem. Cyc.* **11**,173–189.

Melillo, J. M., Aber, J. and Muratore, J. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**, 621–626.

Melillo, J. M. and Gosz, J. 1983. Interactions of biogeochemical cycles in forest ecosystems. In: *The major biogeochemical cycles and their interactions* (eds. B. Bolin and R. B. Cook). John Wiley and Sons, New York, pp. 177–222.

Melillo, J. M, Fruci, J., Houghton, R., Moore III, B. and Skole, D. 1988. Land-use change in the Soviet Union

between 1850 and 1980: causes of a net relase of CO_2 to the atmosphere. *Tellus* **40B**, 116–128.

Melillo, J. M., Steudler, P., Aber, J. and Bowden, R. 1989. Atmospheric deposition and nutrient cycling. In: *Exchange of trace gases between terrestrial ecosystems and the atmosphere* (eds. M. O. Andreae and D. S. Schimel). John Wiley & Sons, Ltd., Dahlem, Konferenzen, pp. 263–280.

Melillo, J. M., Callaghan, T., Woodward, F., Salati, E. and Sinha, S. 1990. Effects of Ecosystems, In: *Climate change: the IPCC scientific assessment* (eds. Houghton, J. T. et al.). Cambridge University Press, Cambridge, New York, pp. 283–310.

Melillo, J. M., McGuire, A., Kicklighter, D., Moore III, B., Vorosmarty, C. and Schloss, A. 1993. Global climate change and terrestrial net primary production. *Nature* **363**, 234–240.

Melillo, J. M., Kicklighter, D., McGuire, A., Peterjohn, W. and Newkirk, K. 1995a. Global change and its effects on soil organic carbon stocks. In: *Dahlem Conference Proceedings*. John Wiley and Sons, New York, pp. 175–189.

Melillo, J. M. 1995b. Human influences on the global nitrogen budget and their implications for the global carbon budget. In: *Toward global planning of sustainable use of the Earth: development of global eco-engineering* (eds. Murai and M. Kimura). Elsevier, Amsterdam, The Netherlands.

Melillo, J. M., Prentice, I., Farquhar, G., Schulze, E.–D. and Sala, O. 1996. Terrestrial biotic responses to environmental change and feedbacks to climate, In: *Climate change 1995: the science of climate change* (eds. J. T. Houghton et al.). Cambridge University Press, pp. 444–481.

Mooney, H. A., Drake, B. G., Luxmoore, R. L., Oechel, W. C. and Pitelka, L. F. 1991. Predicting ecosystem responses to elevated CO_2 concentrations. *BioScience* **41**, 96–104.

NCAR/Navy. 1984. *Global 10-min elevation data.* Digital tape available through National Ocean and Atmospheric Administration, National Geophysical Data Center, Boulder, Colorado, USA.

NCDC (National Climate Data Center). 1992. *1961–1990 monthly station normals tape.* US Department of Commerce, data tape TD 9641.

Nicholls, N., Gruza, G.V., Jouzel, J., Karl, T., Ogallo, L., Parker, D. 1996. Observed climate variability and change. In: *Climate change 1995: the science of climate change* (eds. J. T. Houghton et al.). Cambridge University Press, pp. 132–192.

Pan, Y., McGuire, A., Kicklighter, D. and Melillo, J. 1996. The importance of climate and soils for estimates of net primary production: a sensitivity analysis with the terrestrial ecosystem model. *Global Change Biology* **2**, 5–23.

Pan, Y., Melillo, J., McGuire, A., Kicklighter, D., Pitelka, L., Hibbard, K., Pierce, L., Running, S., Ojima, D., Parton, W., Schimel, D. and other VEMAP members. Modeled responses of terrestrial ecosystems to elevated atmospheric CO_2: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia* 114, 389–404.

Parton, W. J., Scurlock, J., Ojima, D., Gilmanov, T., Scholes, R., Schimel, D., Kirchner, T., Menaut, J.-C., Seastedt, T., Garcia Moya, E, Apinan Kamnalrut and Kinyamario, J. I. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Glob. Biogeochem. Cyc.* **7**, 785–809.

Pastor, J., and Post, W. 1986. Influence of climate, soil moisture and succession on forest soil carbon and nutrient cycles. *Biogeochem.* **2**, 3–27.

Peterjohn, W. T., Melillo, J., Steudler, P., Newkirk, K., Bowles, E. and Aber, J. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol. Appl.* **4**, 617–625.

Pitelka, L.F. and the Plant Migration Workshop Group. 1997. Plant migration and climate change. *American Scientist* **85**, 464–473.

Pickett, S. and White, P. 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, New York.

Post, W. M., King, A. and Wullschleger, S. 1997. Historical variations in terrestrial biospheric carbon storage. *Glob. Biogeochem. Cyc.* **11**, 99–109.

Raich, J. W., Rastetter, E., Melillo, J., Kicklighter, D., Steudler, P., Peterson, B., Grace, A., Moore III, B. and Vorosmarty, C. 1991. Potential net primary productivity in South America: Application of a global model. *Ecol. Appl.* **1**, 399–429.

Rastetter, E. B., Agren, G. I. and Shaver, G. R. 1997. Responses of N-limited ecosystems to increased CO_2: A balanced-nutrition, coupled-element-cycles model. *Ecol. Appl.* **7**, 444–460.

Running, S. W., Nemani, R. and Hungerford, R. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Can. J. of For. Res.* **17**, 472–483.

Running, S. W., and Hunt Jr., E. R. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: *Scaling processes between leaf and landscape levels* (eds. J. R. Ehleringer and C. Field). Academic Press, Orlando, pp. 141–158.

Sarmiento, J. L. and Sundquist, E. T. 1992. Revised budget for the oceanic uptake of anthropogenic carbon dioxide. *Nature* **356**, 589–593.

Schimel, D. S. Braswell, B., Holland, E., McKeown, R., Ojima, D., Painter, T., Parton, W. and Townsend, A. 1994. Climatic, edaphic and biotic controls over storage and turnover of carbon in soils. *Glob. Biogeochem. Cyc.* **8**, 279–293.

Schimel, D. S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology* **1**, 77–91.

Schimel, D. S., et al. 1996a. Radiative forcing of climate change. In: *Climate change 1995: the science of climate*

change (eds. J. T. Houghton et al.). Cambridge University Press. pp. 67–131.

Schimel, D. S., Braswell, B., McKeown, R., Ojima, D., Parton, W. and Pulliam, W. 1996b. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. *Glob. Biogeochem. Cyc.* **10**, 677–692.

Schimel, D. S. et al. 1997. Spatial variability in ecosystem processes at the continental scale: models, data and the role of disturbance. *Ecol. Monog.* **67**, 251–271.

Schindler, D. W., and Bayley, S. E. 1993. The biosphere as an increasing sink for atmospheric carbon: estimates from increased nitrogen deposition. *Glob. Biogeochem. Cyc*. **7**, 717–734.

Schlesinger, W. H. 1991. *Biogeochemistry: an analysis of global change.* Academic, San Diego, Calif.

Schulze, E.-D., DeVries, W., Hauhs, M., Rosén, K., Rasmussen, L., Tann, O.-C. and Nilsson, J. 1989. Critical loads for nitrogen deposition in forest ecosystems. *Water, Air, and Soil Pollut.* **48**, 451–456.

Smith, T. M., and Shugart, H. H. 1993. The transient response of terrestrial carbon storage to a perturbed climate. *Nature* **361**, 523–526.

Solomon, A. M. 1986. Transient response of forests to CO_2-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* **68**, 567–579.

Tans, P., Fung, I. and Enting, I. 1995. Storage versus flux budgets: The terrestrial uptake of CO_2 during the 1980s. In: *Biotic feedbacks in the global climatic system* (eds. G. M. Woodwell and F. T. Mackenzie). Oxford University Press, New York, pp. 351–374.

Tian, H. and Qi, Y. 1990. An analysis on ecological succession processes. In: *Advance in modern ecology* (ed. Ma Shijun). Science Press, Beijing, pp. 90–100.

Tian, H., Xu, H. and Hall, C. 1995. Pattern and change of a boreal forest landscape in the northeastern China. *Water, Air and Soil Pollut.* **82**, 465–476.

Tian, H., Melillo, J.M., Kicklighter, D.W., McGuire, A.D., Helfrich, J., Moore III, B. and Vörösmarty, C.J. 1998a. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**, 664–667.

Tian, H., Hall, C. and Qi, Y. 1998b. Modeling primary productivity of the terrestrial biosphere in changing environments: Toward a dynamic biosphere model. *Critical Reviews in Plant Science* 17, 541–557.

Thompson, M., Randerson, J., Malmstrom, C. and Field, C. 1996. Change in net primary production and heterotrophic respiration: how much is necessary to sustain the terrestrial carbon sink? *Glob. Biogeochem. Cyc.* **10**, 711–726.

Townsend, A. R., Braswell, B., Holland, E. and Penner, J. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecol. Appl.* **6**, 806–814.

Trenberth, K. and Hurrell, J. 1994. Decadal atmosphere-ocean variations in the Pacific. *Clim. Dyn.* **9**, 303–319.

Turner II, B., Clark, W., Kates, R., Richards, J., Mathews, J. and Meyer, W. 1990. *The Earth as transformed by human action.* Cambridge University Press, Cambridge.

Turner D. P., Koerper, G., Harmon, M. and Lee, J. 1995. A carbon budget for forests of the conterminous United States. *Ecol. Appl.* **5**, 421–436.

VEMAP Members. 1995. Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): a comparison of biogeography and biogeochemistry models in the context of global climate change. *Glob. Biogeochem. Cyc.* **9**, 407–437.

Vitousek, P. M. and Howarth, R. W. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochem.* **13**, 87–115.

Vorosmarty, C. J., Moore III, B., Grace, A., Gildea, M., Melillo, J., Peterson, B., Rastetter, E. and Steudler, P. 1989. Continental scale models of water balance and fluvial transport: an application to South America, *Glob. Biogeochem. Cyc.* **3**, 241–265.

Wofsy, S., Goulden, M., Munger, J., Fan, S-M., Bakwin, P., Daube, B., Bassow, S. and Bazzaz. F. 1993. Net exchange of CO_2 in a mid-latitude forest. *Science* **260**, 1314–1317.

Woodward, F. I., Smith, T. M. and Emanuel, W. R. 1995. A global primary productivity and phytogeography model. *Glob. Biogeochem. Cyc.* **9**, 471–490.

Woodwell, G. M. 1995. Will the warming speed the warning? In: *Biotic feedbacks in the global climatic system* (eds. G. M. Woodwell and F. T. Mackenzie). Oxford University Press, New York.

Wullschleger, S. D., Post, W. and King, A. 1995. On the potential for a CO_2 fertilization effect in forests: estimates of the biotic growth factor based on 58 controlled-exposure studies, In: *Biotic feedbacks in the global climatic system* (eds. G. M. Woodwell and F. T. Mackenzie). Oxford University Press, New York, pp. 85–107.

Xiao, X., Kicklighter, D., Melillo, J., McGuire, A., Stone, P. and Sokolov, A. 1997. Linking a global terrestrial biogeochemical model and a 2-D climate model: implications for the global carbon budget. *Tellus* **49B**, 18–37.