Relative Roles of Changes in CO_2 and Climate to Equilibrium Responses of Net Primary Production and Carbon Storage of the Terrestrial Biosphere

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Abstract

In a partial factorial model experiment, we used the Terrestrial Ecosystem Model (TEM, version 4.0) to assess the relative roles of changes in CO_2, temperature, precipitation and cloudiness in equilibrium responses of primary production and carbon storage. In the experiment, we used two levels of atmospheric CO_2 concentration (315 and 522 ppmv CO_2), contemporary climate and changes in temperature, precipitation and cloudiness as estimated by a 3-dimensional atmospheric general circulation model (Geophysical Fluid Dynamic Laboratory-GFDL) and a 2-dimensional climate model (Land-Ocean climate model at Massachusetts Institute of Technology) for doubled CO_2. The results show that elevated CO_2 and projected increases in temperature account for most of the overall equilibrium responses of NPP and carbon storage to changes in climate and CO_2, while the projected changes in precipitation and cloudiness contribute least. This is partly attributable to the magnitudes of changes in CO_2 and climate variables as projected by the climate models. The results also show that the interactions among changes in CO_2 and climate variables play a significant role in the equilibrium responses of NPP and carbon storage to changes in CO_2 and climate. Of all the interaction terms, the interaction between a change in CO_2 and a change in temperature is the most significant.

Keywords: climate change, soil carbon, vegetation carbon, ecosystem model

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I. Introduction

Increases in anthropogenic emissions of greenhouse gases (*e.g.*, CO_2, CH_4, N_2O) have resulted in an increase of the atmospheric abundance of these gases and consequently an increase of radiative forcing of climate (Houghton *et al*., 1995). Atmospheric general circulation models (GCMs) have indicated that the increase of radiative forcing from a doubled CO_2 will change temperature, precipitation and cloudiness of the globe. According to a number of GCMs, equilibrium climate change simulations for a doubled CO_2 will result in increases of global surface mean annual temperature between 1.5 ˚C and 4.5 ˚C (Mitchell *et al*., 1990). The GCMs also project large changes in magnitudes and spatial distributions of precipitation and cloudiness for a doubled CO_2.

Changes in atmospheric CO_2 concentration and climate (temperature, precipitation, solar radiation) are likely to have impacts on the structure and function of the terrestrial biosphere (Gates, 1985; Melillo *et al*., 1990). There are few field experiments on the responses of whole terrestrial ecosystems to elevated CO_2 (Mooney *et al*., 1991) and to climate change, *e.g.*, soil warming (Van Cleve *et al*., 1990; Melillo *et al*., 1995). At present, there is no full-factorial, long-term field experiment to examine the combined effects of changes in individual variables (CO_2 level, temperature, precipitation and solar radiation) and their interactions on terrestrial ecosystems. Our understanding about the sensitivity of net primary production and carbon stock of the terrestrial ecosystems to a change in CO_2 and changes in temperature, precipitation and cloudiness (solar radiation) projected by the climate models is limited to the results of modeling studies.

In earlier sensitivity studies that have used ecosystem models, investigators applied +1 ˚C, +2 ˚C, +4 ˚C warming and/or ±10%, ±20% increase of precipitation uniformly over the globe or continents to estimate the response of NPP (Esser, 1987, 1990; McGuire *et al*., 1993; Zhang, 1993) and carbon storage to climate change (McGuire *et al*., 1996a, 1995; Melillo *et al*., 1995; Schimel *et al*., 1994; Potter *et al*., 1993; Townsend *et al*., 1992; Jenkinson *et al*., 1991; Buol *et al*., 1990). Although this single factor sensitivity analysis approach has been useful for preliminary analyses of the effects of climate change on ecosystems, interpretation of the results have been limited. In reality, changes in climate variables will not be uniform across regions, and GCMs project large latitudinal and longitudinal variations in temperature and precipitation changes for doubled CO_2. By not considering the covariations in climate variables, this approach has the largest inconsistency of the physical climate system and has not taken the effects of other abiotic controls on NPP and carbon storage into account. The interaction between a change in one abiotic factor and changes in other abiotic factors may play an important role in the responses of terrestrial ecosystems to climate change.

To better account for the physical consistency of climate change and the interactions among the driving variables, a number of studies have used the projected changes in temperature, precipitation and cloudiness from GCMs and elevated CO_2 to simulate the potential impacts of climate changes and elevated CO_2 on primary production and carbon storage of natural and managed ecosystems at global and continental scales (Melillo *et al*., 1993; Parton *et al*., 1995; Rosenzweig and Parry, 1994; VEMAP Members, 1995; Xiao *et al*., 1996). Both the magnitude and spatial distribution of responses of net primary production (NPP) and carbon storage vary among climate change predictions as estimated by GCMs for an particular ecosystem model. The responses of NPP and carbon storage also vary among various ecosystem models for a given climate change prediction (VEMAP Members, 1995). The differences in responses of NPP and carbon storage may be attributable to the concepts and formulations of the ecosystem models and climate models used in the studies. One of the earlier studies also showed that the response of net primary production of the terrestrial biosphere is affected strongly by the interaction between a change in atmospheric CO_2 concentration and a change in climate (Melillo *et al*., 1993). Although this approach provides estimates of the overall responses of NPP and carbon storage to changes in the four driving variables, the relative contribution of a change in an individual variable and its interactions with changes of the other three variables to the overall responses of NPP and carbon storage have not been quantified.

Uncertainties in future concentrations of atmospheric CO_2 and projected changes in temperature, precipitation and cloudiness by GCMs are large and differ among the four variables. Different ecosystems may have different responses to changes in CO_2, temperature, precipitation and cloudiness. Quantification of the effect of a change in an individual driving variable, including its interaction with changes of other driving variables, on NPP and carbon storage will further our understanding of responses of ecosystems to climate change and how well ecosystem models represent ecosystem processes. In addition, we will gain a better understanding of the importance of the uncertainties in changes of climate variables estimated by GCMs on ecosystems.

In this study, we conduct a partial factorial experiment of model simulations, using a global biogeochemistry model (Terrestrial Ecosystem Model - TEM 4.0; McGuire *et al*., 1995a, 1996b) to quantify the relative importance of projected changes in temperature, precipitation, cloudiness and atmospheric CO_2 concentration to the equilibrium responses of NPP and carbon storage of terrestrial ecosystems. We used two levels of atmospheric CO_2 concentration (315 ppmv and 522 ppmv) and changes in temperature, precipitation and cloudiness projected by a 3-dimensional GCM (Geophysical Fluid Dynamic Laboratory - GFDL; Manabe and Wetherald, 1987; Wetherald and Manabe, 1988) and a 2-dimensional statistical-dynamical climate model (Land-Ocean climate model at Massachusetts Institute of Technology (MIT L-O); Sokolov and Stone, 1995). Both the 2-D MIT L-O climate model and TEM are linked in an integrated impact assessment framework of climate change at Massachusetts Institute of Technology (Prinn *et al*., 1996; Xiao *et al*., 1996). A comparison of the responses of primary production and carbon storage to climate change predictions between the 3-D GFDL GCM and the 2-D MIT L-O climate model provide insights into the importance of spatial resolutions, including longitudinal variations of climate change predictions, on estimating ecosystem responses to climate change (Xiao *et al*., 1996). To explore how ecosystem responses vary over different spatial scales, we examined the responses of NPP, reactive soil organic carbon and vegetation carbon across the scales of the globe, latitudinal bands and biomes.

II. The Terrestrial Ecosystem Model (TEM)

The TEM (Raich *et al*., 1991; McGuire *et al*., 1992, 1993, 1995a, 1996a, 1996b) is a process-based ecosystem model that simulates important carbon and nitrogen fluxes and pools for various terrestrial ecosystems (Fig. 1). It runs at a monthly time step. Driving variables include monthly mean climate (precipitation, temperature and cloudiness), soil texture (sand, clay and silt proportion), elevation, vegetation and water availability. The water balance model of Vorosmarty *et al*., (1988) is used to generate hydrological input (*e.g.*, potential evapotranspiration, soil moisture) for TEM. In this study, we used version 4.0 of TEM (McGuire *et al*., 1995a, 1996b). Here, we briefly review how TEM describes the influence of CO_2, temperature, precipitation and cloudiness on primary production and carbon stocks.

Net primary production (NPP) is calculated as the difference between gross primary production (GPP) and plant respiration (R_A). The flux GPP is calculated at each monthly time step as follows:

$$GPP = Cmax\ f(PAR)\, f(LEAF)\, f(T)\, f(CO_2, H_2O)\, f(NA) \quad (1)$$

where Cmax is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF is leaf area relative to maximum annual leaf area, T is temperature, CO_2 is atmospheric CO_2 concentration, H_2O is water availability, and NA is nitrogen availability.

The effect of CO_2 and water availability on GPP are interrelated. The function $f(CO_2, H_2O)$ is described by the hyperbolic relationship:

$$f(CO_2, H_2O) = Ci\ /\ (kc + Ci) \quad (2)$$

where Ci is the concentration of CO_2 within leaves of the canopy and kc is the half-saturation constant for CO_2 uptake by plants. The relationship between CO_2 concentration inside stomatal cavities (Ci) and in the atmosphere (Ca) is directly proportional to relative moisture availability (Raich *et al*., 1991):

$$Ci = GvCa \qquad (3a)$$

$$Gv = 0.1 + (0.9\ \mathrm{EET/PET}) \qquad (3b)$$

where Gv is a unitless multiplier that accounts for changes in leaf conductivity to CO_2 resulting from changes in moisture availability, PET is potential evapotranspiration and EET is the estimated evapotranspiration. The flux PET is calculated as a function of mean air temperature and solar radiation (Jensen and Haise, 1963). The flux EET is equal to PET in wet months but is modeled as a function of rainfall, snowmelt recharge and a change of soil moisture in dry months (Vorosmarty, 1989).

The results from CO_2-enrichment studies indicate that the response of plant productivity to doubled CO_2 ranges from 20% to 50%, given adequate nutrients and water (Kimball, 1975; Gates, 1985; McGuire *et al*., 1995b). In TEM, the parameter kc (400 ppmv) has been chosen to increase $f(CO_2, H_2O)$ by 37% for a doubling of atmospheric CO_2 concentration from 340 ppmv to 680 ppmv, with canopy conductance equal to 1 (McGuire *et al*., 1992, 1993). It is important to note that the response of GPP to doubled CO_2 is not a constant 37% for kc of 400 ppmv, because GPP calculation is also affected by f(NA), which represents the limiting effect of vegetation nitrogen status on GPP (McGuire *et al*., 1992, 1993; Melillo *et al*., 1993). Vegetation nitrogen status is determined by vegetation nitrogen uptake (NUPTAKE) and nitrogen from the labile nitrogen pool of vegetation (NMOBIL). The nitrogen down-regulation of GPP response to elevated CO_2 in TEM is discussed elsewhere (McGuire *et al*., 1996b).

Increasing irradiance of PAR increases GPP hyperbolically in the following form: f(PAR) = PAR / (ki + PAR). A mean value of 314 J $cm^{-2}d^{-1}$ for ki from published leaf studies is used and applied to entire leaf canopies independent of vegetation types (Raich *et al*., 1991). Cloudiness affects the amount of solar irradiance, including PAR, that reaches the canopy of vegetation.

The effect of air temperature on GPP is described by allowing f(T) to increase in a parabolic fashion to a grid-cell specific optimum temperature. Between the optimum temperature and a maximum vegetation-specific temperature constraint, f(T) is equal to 1.0. Above the maximum temperature constraint, f(T) declines rapidly to 0.0 (McGuire *et al*., 1996b). Air temperature also affects plant respiration (R_A). The flux R_A includes both maintenance respiration (R_M) and construction respiration (R_C). The flux R_M increases logarithmically with temperature using a Q_{10} value that varies from 1.5 to 2.5 (McGuire *et al*., 1992). The flux R_C is determined to be 20% of the difference between GPP and R_M (Raich *et al*., 1991). Thus, changes in NPP are directly related to changes in CO_2, temperature, precipitation and cloudiness.

In TEM, the amount of carbon stored in vegetation and soils is a balance between carbon fluxes into and out of these pools (Fig. 1). To attain equilibrium conditions in the simulation, annual fluxes out of a carbon pool must equal annual fluxes into the pool. Vegetation carbon increases with NPP, but decreases with litterfall. Although litterfall is simply modeled as a function of biomass with no independent climate and CO_2 effects, annual litterfall must equal annual NPP to maintain equilibrium conditions in the simulation. Thus, climate and CO_2 have an indirect effect on litterfall. Soil organic carbon increases with litterfall, but decreases with decomposition (*i.e.*, heterotrophic respiration, R_M). The flux R_M represents decomposition of all organic matter in the ecosystem. It is modeled as a function of soil carbon (C_s), mean monthly air temperature (T), mean volumetric soil moisture and the gram-specific decomposition constant k_d (Raich *et al*., 1991):

$$R_H = k_d \, (C_s) \, e^{0.0693T} \; \text{MOIST} \tag{4}$$

where MOIST is a parabolic function of volumetric soil moisture (McGuire *et al*., 1996b).

Thus, changes in heterotrophic respiration depend directly on changes in temperature and precipitation. Changes in CO_2 and cloudiness also indirectly influence decomposition of soil organic matter by affecting litterfall and the resulting amount of soil organic matter to be decomposed.

III. Design of Simulation Runs

In this study, we designed a partial factorial experiment (Table 1) to efficiently illustrate the combined effects of a change in an individual variable and its interactions with changes of other variables on the overall responses of NPP and carbon storage of the terrestrial biosphere to changes in CO_2 and climate. We first ran TEM for contemporary climate with 315 ppmv CO_2 as the baseline. Next, we ran TEM for complete climate change at 522 ppmv CO_2 (see #1, #6 in Table 1), which is considered as the full response model for our comparison in this study. Third, we ran four TEM simulations (see #2-5, #7-10 in Table 1). In each of the four simulations, one of the four driving variable (CO_2, temperature, precipitation, cloudiness) uses the baseline values (*i.e.*, contemporary climate, 315 ppmv CO_2), while the other three variables use values from the climate change predictions or elevated CO_2. Eliminating a change in an individual variable in a simulation (*e.g.*, ΔCO_2) will result in losses of both the effect of the change in this variable (*i.e.*, ΔCO_2) and the effect of its interactions with changes of other variables, *i.e.*, temperature ($\Delta CO_2 \times$

ΔT), precipitation ($\Delta CO_2 \times \Delta P$) and cloudiness ($\Delta CO_2 \times \Delta C$). This approach has the least inconsistency in physical climate system and includes the interactions among changes of three variables. Therefore, this subset of six model runs out of sixteen runs required in a full factorial experiment (4 factors at 2 levels) allows us to efficiently explore the relative contribution of a change in each of the four driving variables to the overall responses of primary production and carbon storage of the terrestrial biosphere. In the data analysis, we compare the results from the complete climate change at 522 ppmv CO_2, to the four simulations that use the baseline values for one of the four driving variables. This comparison illustrates the combined effects of a change in an individual variable and its interactions with changes of the other three variables to the overall responses of primary production and carbon storage of terrestrial ecosystems.

To determine the relative contribution of the interaction between elevated CO_2 and climate change to ecosystem responses, we compare the results among the following three simulations: (1) complete climate change at 522 ppmv CO_2; (2) the scenario with no change in CO_2 (complete climate change at 315 ppmv CO2); and (3) contemporary climate at 522 ppmv CO_2, which is an additional TEM simulation to estimate the effect of elevated CO_2 alone on primary production and carbon storage (Table 1). For examining the effects of changes in CO_2 and climate at the global and biome scales, we may conceptualize that the responses of net primary production to complete climate change at 522 ppmv CO_2 ($\Delta NPP_{\Delta CO_2,\, \Delta climate}$) are represented by elevated CO_2 (ΔCO_2), climate change (Δclimate), and their interactions ($\Delta CO_2 \times \Delta$climate):

$$\Delta NPP_{\Delta CO_2,\, \Delta climate} = a_0 + a_1 \Delta CO_2 + a_2 \Delta climate + a_3 \Delta CO_2 \times \Delta climate \tag{5}$$

We can then calculate the effects of interactions on NPP as the following:

$$\Delta NPP_{\Delta CO_2 \times \Delta climate} = \Delta NPP_{\Delta CO_2,\, \Delta climate} - \Delta NPP_{\Delta CO_2} - \Delta NPP_{\Delta climate} \tag{6}$$

where $\Delta NPP_{\Delta CO_2 \times \Delta climate}$ is the interaction between elevated CO_2 and climate change, $\Delta NPP_{\Delta CO_2}$ is NPP response to contemporary climate at 522 ppmv CO_2, and $\Delta NPP_{\Delta climate}$ is NPP response to complete climate change at 315 ppmv CO_2. The same approach is used for vegetation carbon and soil carbon storage.

For global extrapolation, TEM uses spatial data sets that are gridded at a resolution of 0.5˚ latitude by 0.5˚ longitude. The global data sets include long-term average contemporary climate data from the Cramer and Leemans climate database (Cramer, personal communication), potential vegetation (Melillo *et al*., 1993), soil texture (FAO-UNESCO, 1971) and elevation (NCAR/Navy, 1984). The Cramer and Leemans climate data sets are an update of the Leemans and Cramer climate data sets (Leemans and Cramer, 1990). These spatial data sets contain 62,483 land grid cells, including 3,059 ice grid cells and 1,525 wetland grid cells. Geographically, the global data sets cover land areas from 56 ˚S to 83 ˚N.

For climate change scenarios, we use climate outputs for 1×CO_2 and 2×CO_2 simulations from the 3-dimensional GFDL GCM (Weatherald and Manabe, 1988) and the 2-dimensional MIT L-O climate model (Sokolov and Stone, 1995). The 3-D GFDL GCM has a spatial resolution of 7.5˚ (longitude) × 4.44˚ (latitude). The 2-D MIT L-O climate model simulates the zonally averaged climate separately over land and ocean as a function of latitude and height (Yao and Stone, 1987; Stone and Yao, 1987, 1990; Sokolov and Stone, 1995). The 2-D model has 23 latitude bands, corresponding to a resolution of 7.826˚, and nine vertical layers. Detailed descriptions of the 2-D MIT L-O climate model for climate change predictions are documented in Sokolov and Stone (1995). The climate output of GFDL has been interpolated to 0.5˚ × 0.5˚ grid cells by applying a spherical interpolation routine to the data (Willmott *et al*., 1985). For the climate output of the 2-D MIT L-O climate model, we apply the zonally averaged data over land to all 0.5˚ × 0.5˚ grid cells within the latitudinal band.

Globally-averaged changes in climate variables projected by the 3-D GFDL are in the middle of the range of changes projected by a number of GCMs for doubled CO_2. The globally-averaged changes in climate variables estimated by the 2-D MIT L-O climate model for doubled CO_2 are similar to GFDL, although they operate at very different spatial domains. Globally, the GFDL GCM projects a change of +4.0 °C for mean annual temperature, +8.3% for annual precipitation and -0.7% for mean annual cloudiness. The 2-D MIT L-O climate model projects a change of +4.2 °C for mean annual temperature, +11.5% for annual precipitation and -2.6% for mean annual cloudiness. Latitudinal distributions in the changes of temperature, precipitation and cloudiness between the GFDL and MIT L-O have similar patterns (Fig. 2). In an earlier study (Xiao *et al*., 1996), we compared the responses of NPP and carbon storage to climate changes represented by two 3-dimensional GCMs (*i.e.*, GFDL, Wetherald and Manabe, 1988; Goddard Institute for Space Studies - GISS, Hansen *et al*., 1983, 1984) and the 2-D MIT L-O climate model (see Sokolov and Stone, 1995). The simulation results have shown that the global responses of NPP and total carbon storage are generally similar among the climate change predictions from the 3-D GCMs and the 2-D MIT L-O climate model.

We used the following procedure to generate "future climate." First, we calculated absolute differences in monthly mean temperature, ratios in monthly precipitation and ratios in monthly mean cloudiness between the 2×CO_2 simulation and the 1×CO_2 simulation of each model. Then, we added the absolute differences in monthly mean temperature between the 2×CO_2 and 1×CO_2 simulations to the contemporary monthly temperature data; and multiplied the ratios in monthly precipitation and monthly mean cloudiness between the 2×CO_2 and 1×CO_2 simulations to the contemporary monthly precipitation and cloudiness data, respectively. For elevated CO_2 level, we used an atmospheric CO_2 concentration of 522 ppmv as corresponding to an effective CO_2 doubling associated with the radiative forcing (Xiao *et al*., 1996).

In this study, we ran TEM to equilibrium for each simulation. Therefore, the estimates of carbon and nitrogen fluxes and pool sizes apply only to mature, undisturbed vegetation and ecosystems. Effects of land use and management on carbon and nitrogen dynamics are not considered.

IV. Response of NPP to Climate Change and Elevated CO_2

IV.1 Relative Roles of Changes in CO_2, Temperature, Precipitation and Cloudiness

The TEM estimates global annual NPP to be 47.9 PgC yr^{-1} for contemporary climate with 315 ppmv CO_2. For complete climate change at 522 ppmv CO_2, the global NPP response is +18.5% for the GFDL climate (see Tg, Pg, Cg, 522 in Table 2) and +17.8% for the 2-D L-O climate (see Tm, Pm, Cm, 522 in Table 3), respectively. Among the four simulations with the GFDL climate that use the baseline values for one variable, global NPP increases by 0.7% for the scenario with no change in CO_2 (see Tg, Pg, Cg, 315 in Table 2); 7.7% for the scenario with no change in temperature (see Tcl, Pg, Cg, 522 in Table 2); 17.8% for the scenario with no change in precipitation (see Tg, Pcl, Cg, 522 in Table 2); and 19.0% for the scenario with no change in cloudiness (see Tg, Pg, Ccl, 522 in Table 2).

The difference in global NPP responses between the scenario of the complete climate change at 522 ppmv CO_2 and one of the four scenarios that uses the baseline values for one variable indicates the combined effect of a change in an individual variable and its interactions with changes in other variables on the overall response of global NPP, *i.e.*, the relative role of a change in an individual variable The difference ranges from –0.5% (18.5% – 19.0%) for the scenario with no change in cloudiness to 17.8% (18.5% – 0.7%) for the scenario with no change in CO_2. Thus, the larger difference indicates a larger contribution of the change in CO_2 to the overall NPP response. The results show that with the TEM, elevated CO_2 contributes substantially, an increase in temperature contributes moderately, and changes in precipitation and cloudiness contribute little to the overall response of global NPP. Global NPP responses for the simulations using the 2-D L-O climate (Table 3) have patterns similar to those for the GFDL climate (Table 2).

Along the 0.5˚ resolution latitudinal bands, NPP has a bimodal distribution for complete climate change at 522 ppmv CO_2 for both the GFDL climate (Fig. 3a) and the MIT L-O climate (Fig. 3b). There are large increases in both tropical regions and the mid-latitude in the northern hemisphere. In the latitudinal bands dominated by arid biomes, including the Sahara desert (*i.e.*, 10 ˚N to 25 ˚N), the response of NPP to complete climate change at 522 ppmv CO_2 is more limited. For the scenario with no change in CO_2, NPP decreases in the tropical regions but increases in the mid-latitude temperate zones (Fig. 3). For the scenario with no temperature increase, NPP response is large in tropical regions, but small in mid- to high- latitudes (Fig. 3). The latitudinal distributions of NPP response for the scenario with no change in precipitation and the scenario with no change in cloudiness are similar to the latitudinal distribution of NPP response to complete climate change at 522 ppmv CO_2. Thus, the changes in precipitation and cloudiness projected by the climate models contribute little to the overall response of NPP along the latitudinal bands.

In TEM, NPP of mid- and high- latitude ecosystems is primarily limited by nitrogen availability. The results indicate that the response of NPP in these regions is controlled primarily by temperature increase and secondarily by elevated CO_2. Increases of temperature and precipitation in mid- and high- latitudes enhance decomposition of soil organic matter. As a result, more nitrogen is released from soils to be available for plant uptake, and thus plant production increases. The changes in temperature estimated by the climate models have a larger effect on the decomposition of soil organic matter than the predicted changes in precipitation. In the tropic regions, NPP of moist tropical ecosystems is generally not limited by nitrogen availability. The response of NPP in tropical regions is controlled primarily by elevated CO_2 and secondarily by temperature increase. Although NPP in arid regions (*i.e.*, 10 ˚N to 25 ˚N) is limited by water availability, the NPP responses for the scenario with no change in precipitation indicate that the effect of projected changes in precipitation is small in arid regions. Temperature also has a small effect on NPP response in arid regions. Elevated CO_2 appears to account for most of the NPP response in the arid regions as a result of enhanced water use efficiency. The NPP response for the scenario with no change in cloudiness is slightly larger than the NPP response to complete climate change at 522 ppmv CO_2 (Fig. 3). The degree of cloudiness in the contemporary climate is greater than that projected for the future by the GFDL GCM and the MIT L-O climate model. In TEM, lower cloudiness increases the amount of solar radiance, including PAR. Enhanced PAR has the potential to increase GPP and NPP. Enhanced solar radiation also increases PET. High PET may reduce soil moisture and thus increase water stress of plant to potentially decrease GPP and NPP. The results indicate that the effect of enhanced radiation-induced water stress is larger than the effect of increased PAR.

The latitudinal distributions of NPP responses to the GFDL climate are similar to the latitudinal distributions of NPP responses to the MIT L-O climate, except at high latitudes. The largest differences in NPP responses occur within the 50.5 – 58.5 ˚N and 66.5 – 74.0 ˚N latitudinal bands, where the MIT L-O climate model projects relatively larger increases in temperature and cloudiness than the GFDL GCM (Fig. 2). The comparison of NPP responses among the scenario with no temperature change, the scenario with no cloudiness change and the scenario with precipitation change indicates that the differences in NPP responses at high latitudes between the GFDL climate and MIT L-O climate are primarily due to larger increases in temperature projected by the MIT L-O climate model (Fig. 2).

At the biome scale, the response of NPP varies among the 18 vegetation types. NPP increases substantially in all biomes for complete climate change at 522 ppmv CO_2, ranging from +13.6% in tropical evergreen forest to 30.0% in wet/moist tundra for the GFDL climate (Table 2) and from 12.7% in tropical deciduous forest to 36.5% in desert for the MIT L-O climate (Table 3). For the scenario with no change in CO_2, climate change projected by the GFDL results in a decrease of NPP in tropical ecosystems and arid ecosystems ranging from –12.5% in desert to –0.9% in tropical savanna, but an increase of NPP for the other biomes, ranging from +3.3% in temperate mixed forest to +24.1% in wet/moist tundra (Table 2). The results indicate that percent response of NPP to a change in CO2 is most sensitive in deserts and the least sensitive in wet/moist tundra. Elevated CO_2 significantly increases water use efficiency of plants in arid lands. Although percent NPP responses in moist tropical ecosystems are moderate, the absolute changes of NPP in tropical ecosystems are substantial, because NPP per unit area in tropical ecosystems is much larger than it is in deserts and arid shrublands.

For the scenario with no change in temperature, NPP increases for the 18 biomes, ranging from 2.5% in boreal forest to 29.3% in desert for the GFDL-q climate (Table 2), and from 0.5% in wet/moist tundra to 31.8% in desert for the MIT L-O climate (Table 3). The NPP response for the scenario with no temperature increase is much smaller than the NPP response for complete climate change with 522 ppmv CO_2, except for arid ecosystems (*e.g.*, desert, arid shrubland) where water is the dominant limiting factor and soil organic matter is low (Table 2). Thus, NPP of most ecosystems is sensitive to changes in temperature. The NPP response to changes in temperature estimated by GFDL is the most sensitive in boreal forest and the least sensitive in desert.

The NPP responses for the scenario with no change in precipitation and the scenario with no change in cloudiness are similar to the NPP responses to complete climate change at 522 ppmv CO_2 for all 18 biomes. These results indicate that projected changes in precipitation and cloudiness by the climate models have little effect on NPP at the biome scale. The responses of NPP for the scenario with no change in cloudiness are slightly higher than NPP responses to complete climate change at 522 ppmv CO_2. As contemporary climate has slightly higher cloudiness, the results indicate that the effect of enhanced radiation-induced water stress to plants is larger than the effect of increasing PAR for all biomes.

IV.2 The Interaction Between Elevated CO_2 and Climate Change

The interaction between elevated CO_2 and climate change contributes about 10.2% to the overall response (18.5%) of global NPP to complete climate change at 522 ppmv CO_2 in the GFDL climate (Table 2). Similarly, the interaction between elevated CO_2 and climate change contributes 9.5% to the overall response (17.8%) of global NPP to complete climate changes at 522 ppmv CO_2 in the MIT L-O climate (Table 3). Globally, the interaction between elevated CO_2 and climate change has a larger contribution to the overall response of NPP than the effect of elevated CO_2 alone. In conjunction with the analyses on the relative role of changes in CO_2, temperature, precipitation and cloudiness in the previous section, the results show that the interaction between elevated CO_2 and climate change is primarily determined by the interaction between elevated CO_2 and temperature change. Higher temperature results in enhanced decomposition of soil organic matter (see Eq. 4) to make more nitrogen available in soils for plant uptake. Both higher temperature and elevated CO_2 may increases GPP (see Eqs. 1, 2, 3). Therefore, NPP increases substantially for the scenarios including both elevated CO_2 and temperature change, because more carbon (CO_2) and nitrogen are available.

At the biome scale, the interaction between elevated CO_2 and climate change is important but its contribution to the overall NPP response varies among the biomes (Tables 2, 3). In tropical evergreen forest, the interaction between elevated CO_2 and climate change plays a dominant role and is much larger than both the effect of climate change and the effect of elevated CO_2 alone. In boreal forests, climate change plays the largest role, the interaction between elevated CO_2 and climate change an intermediate role, and elevated CO_2 the least role. In contrast, the interaction between elevated CO_2 and climate change in dry ecosystems (desert, arid shrubland, xeromorphic forest) is much smaller than the effect of elevated CO_2 alone. The contribution of the interaction between elevated CO_2 and climate change to the overall NPP response of the 18 biomes varies between the 3-D GFDL climate and 2-D MIT L-O climate, especially for high latitude ecosystems. Geographical distributions of climate changes differ between the climate models and affect the contributions of the interaction between elevated CO_2 and climate change to the overall NPP responses at larger spatial scale.

V. Response of Vegetation Carbon to Climate Change and Elevated CO_2

The TEM estimates global vegetation to be 909 PgC for contemporary climate with 315 ppmv CO_2. Global vegetation carbon increases substantially for the complete climate change with 522 ppmv CO_2: +18.3% (166 PgC) for the GFDL climate and +17.3% (157 PgC) for the MIT L-O climate.

The responses of vegetation carbon (Tables 4, 5, Fig. 4) have patterns similar to the NPP responses at the scales of latitudinal bands and biomes. An increase in NPP results in an increase in vegetation carbon. The responses of vegetation carbon are similar between the GFDL climate and MIT L-O climate, except at high latitudes (Fig. 4). The largest differences in vegetation carbon response between the GFDL climate and the MIT L-O climate occur within the 50.5 – 58.5 ˚N and 66.5 – 74.0 ˚N latitudinal bands, where the MIT L-O climate model projects relatively larger increases in temperature and cloudiness than the GFDL GCM (Fig. 2).

Similar to the relationship between the responses of NPP and vegetation carbon described above, the patterns of the relative contribution of the interaction between elevated CO_2 and climate change to the overall response of vegetation carbon to complete climate change at 522 ppmv CO_2 are essentially the same as those described for NPP.

VI. Response of Soil Organic Carbon to Climate Change and Elevated CO_2

VI.1 Relative Role of Changes in CO_2, Temperature, Precipitation and Cloudiness

Version 4.0 of TEM defines a reactive soil carbon pool that excludes biologically "inert" soil organic matter. The TEM estimates that global reactive soil organic carbon at equilibrium is 750 PgC for contemporary climate with 315 ppmv CO_2, which is about 50% of the 1500 PgC estimated by several inventories of soil organic carbon up to 1-meter depth (Schlesinger, 1977; Post *et al*., 1982; Eswaran *et al*., 1993).

For complete climate change at 522 ppmv CO_2, global reactive soil organic carbon decreases moderately by –4.0% (30 PgC) for the GFDL climate (Table 6) and by –5.6% (42 PgC) for the MIT L-O climate (Table 7). For the scenario with no change in CO_2, global reactive soil organic carbon decreases substantially, *i.e.*, –15.0% (112 PgC) for the GFDL climate and –17.2% (129 PgC) for the MIT L-O climate. For the scenario with no change in temperature, global reactive soil organic carbon increases moderately by +4.8% (36 PgC) for the GFDL climate and +5.0% (38 PgC) for the MIT L-O climate, respectively. Global reactive soil organic carbon decreases moderately for the scenario with no change in precipitation and the scenario with no change in cloudiness (Tables 6, 7).

A comparison of the responses of soil organic carbon between the scenario of complete climate change at 522 ppmv CO_2 and the four scenarios that use baseline values for one of the four driving variables indicates that temperature increase and elevated CO_2 contribute the most to the response of reactive soil organic carbon. The changes in precipitation and cloudiness contribute little to the loss of reactive soil organic carbon. In TEM, an increase in temperature enhances decomposition of soil organic matter, resulting in an decrease of soil organic carbon. Elevated CO_2 increases NPP, which then increases litterfall. More input of litterfall to soils would increase soil organic carbon. Globally, the responses of reactive soil organic carbon in the MIT L-O climate are slightly larger than those in the GFDL climate. This difference in response is attributable to relatively larger temperature increases projected by the MIT L-O climate model.

Along the 0.5˚ resolution latitudinal bands, changes in reactive soil organic carbon vary slightly for the complete climate change at 522 ppmv CO_2, with relatively larger decreases in mid- latitudes. Reactive soil organic carbon has the largest decrease for the scenario with no change in CO_2. In contrast, reactive soil organic carbon increases in all latitudinal bands for the scenario with no change in temperature. The responses of reactive soil organic carbon for the scenario with no change in precipitation and the scenario with no change in cloudiness are similar to that for the complete climate change at 522 ppmv CO_2 (Fig. 5). In general, the loss of reactive soil organic carbon is relatively larger in mid- to high- latitudes in the northern hemisphere than in tropical regions for the scenarios with temperature increase (Fig. 5). For doubled CO_2, both the GFDL and MIT L-O climate models project that increases in temperatures are larger in the mid- and high- latitudes than in tropical regions (Fig. 2). Latitudinal distributions of reactive soil organic carbon for the GFDL climate are similar to those for the MIT L-O climate, except at high latitudes of the northern hemisphere, where loss of soil organic carbon is substantially larger for the MIT L-O climate than for the GFDL climate (Fig. 5). This is attributable to the relatively larger temperature increases at high latitudes projected by the MIT L-O climate model (Fig. 2). The projected temperature increases at high latitudes by the MIT L-O climate model are similar to those for the UKMO climate (Wilson and Mitchell, 1987).

At the biome scale, reactive soil organic carbon decreases in the 18 biomes for complete climate change at 522 ppmv CO_2, ranging from –0.3% in polar desert/alpine tundra to –8.0% in tropical savanna for the GFDL climate (Table 6), and from –0.3% in temperate coniferous forest to –15.1% in boreal woodlands for the MIT L-O climate (Table 7). All biomes lose soil organic carbon for the scenario with no change in CO_2, but accumulate soil organic carbon for the scenario with no change in temperature (Table 6). The dry ecosystems (desert, arid shrubland, xeromorphic forest and Mediterranean shrubland) gain more soil organic carbon than the other ecosystems in the scenario with no change in temperature, because of reduced water stress on production in the dry regions. A comparison of responses of soil organic carbon between the scenario of complete climate change at 522 ppmv CO_2 and the scenario with no precipitation change indicates that the increase of precipitation projected by the climate models slightly enhances decomposition of reactive soil organic carbon for the 18 biomes. A decrease of cloudiness has a minor effect on reactive soil organic carbon. Large differences in loss of reactive soil organic carbon between the GFDL climate and the MIT L-O climate occur in higher latitude ecosystems, for instance, boreal forest, boreal woodland, wet/moist tundra (Tables 6, 7). Again, this is attributable to a larger temperature increase in high latitudes projected by the 2-D MIT L-O climate model (Fig. 2).

VI.2 The Interaction Between Elevated CO_2 and Climate Change

At the global scale, the response of reactive soil organic carbon to complete climate change at 522 ppmv CO_2 is dominated by the loss of soil organic carbon caused by the temperature increase (Tables 6, 7). The compensating effects of elevated CO_2 and the interaction between elevated CO_2 and climate change reduce the amount of soil organic carbon that could potentially be lost from terrestrial ecosystems. Globally, the contribution of the interaction between elevated CO_2 and climate change to the overall response of reactive soil organic carbon under complete climate change at 522 ppmv CO_2 is 5.5% for the GFDL climate and 6.1% MIT L-O climate, respectively, which are equal or slightly larger than the contribution (5.5%) from the main effect of elevated CO_2 (Tables 6, 7). The interaction between elevated CO_2 and climate change represents the effect of enhanced NPP and litterfall on soil organic carbon pool caused by elevated CO_2 and temperature increase.

At the biome scale, the interaction between elevated CO_2 and climate change has different roles in the overall response of soil organic carbon among the 18 biomes (Tables 6, 7). In dry biomes (desert, arid shrubland, xeromorphic forest, Mediterranean shrubland), the interaction between elevated CO_2 and climate change plays a much smaller role than the main effect of elevated CO_2. In contrast, the interaction between elevated CO_2 and climate change in tropical evergreen forest and boreal forest play a larger role than the main effect of elevated CO_2. This is related to the fact that NPP in the dry biomes is primarily controlled by water availability and the amounts of soil organic matter in the dry biomes are much smaller than tropical evergreen forest and boreal forest (Tables 6, 7). The contribution of the interaction between elevated CO_2 and climate change varies between the 3-D GFDL and the 2-D MIT L-O climate model. Therefore, the differences in the geographical distributions of climate change among climate models does affect the relative contribution of the interaction between elevated CO_2 and climate change to the overall responses of reactive soil organic carbon at larger spatial scales.

VII. Discussion

VII.1 Effects of the Magnitudes of Changes in CO_2 Level and Climate

The TEM results show that elevated CO_2 and temperature change contribute large proportions to the overall responses of NPP and carbon storage to changes in CO_2 and climate, while precipitation and cloudiness changes contribute small proportions. This is attributable to the magnitude of changes in CO_2, temperature, precipitation and cloudiness projected by the

GCMs. In an earlier study that used alternative input data sets of contemporary climate, solar radiation and soil texture for the conterminous United States to drive TEM (Pan *et al*., 1996), results show that the differences in NPP estimates depend in part on the magnitude of differences among the input data sets. The projected changes in global annual mean temperature, annual precipitation and annual mean cloudiness are similar between the GFDL and MIT L-O climate models. Other GCMs have also projected similar magnitudes of climate change for doubled CO_2. For example, the GISS GCM projected +4.2 ˚C in global mean annual temperature, +11.0% in annual precipitation and -3.4% in mean annual cloudiness (Hansen *et al*., 1983, 1984). The OSU GCM projected +2.8 ˚C in global mean annual temperature, +7.8% in annual precipitation and –3.4% in mean annual cloudiness (Schlesinger and Zhao, 1989). Major differences among GCMs occur in spatial patterns of projected changes of temperature, precipitation and cloudiness, especially in precipitation (Cramer and Leemans, 1993). As shown in this study, the responses of NPP, vegetation carbon and reactive soil organic carbon are slightly different between the 3-D GFDL climate and the 2-D MIT L-O climate across the scales of the globe, latitudinal bands and biomes, except at high latitudes.

This study indicates that CO_2 fertilization plays an important role in primary production and the global carbon budget. This is consistent with previous analyses using the TEM (Melillo *et al*., 1993, 1995). A number of studies have suggested that CO_2 fertilization is one of the major mechanisms that account for the global carbon budget (Gifford, 1993). For the global carbon budget in the decade of 1980–1989, approximately 1.8 PgC/yr of anthropogenic emissions of carbon cannot be balanced with known carbon sinks and sources (Siegenthaler and Sarmiento, 1993). The estimates of the effect of global CO_2 fertilization for the 1980s are ~1.2 PgC/yr (Rotmans and den Elzen, 1993), <1.5 PgC/yr (Friedlingstein *et al*., 1995), and 1 PgC/yr or less (Schimel, 1995). The estimate of the effect of CO_2 fertilization on carbon storage in 1990 is about 1 PgC/yr (Melillo *et al*., 1996). However, these studies have not considered the possible effects of interactions among changes in CO_2 and climate variables on carbon storage. Our results show that CO_2 fertilization is influenced by climate change across the scales of the globe, latitudinal bands and biomes. At the global scale, the interaction between elevated CO_2 and climate change has approximately an equal effect on the responses of NPP and carbon storage as the effect of elevated CO_2 alone.

Our study also indicates that temperature change estimated by the climate models play an important role in responses of NPP and carbon stocks. The changes in annual mean temperature estimated by the GFDL and MIT L-O climate models for doubled CO_2 are large, *e.g.*, globally +4.0 ˚C by GFDL and +4.2 ˚C by MIT L-O. Increased temperature affects plant photosynthesis, plant respiration and water availability in soils. Increased temperature also affects the rates of temperature-dependent soil processes, *e.g.*, decomposition and net nitrogen mineralization. In a soil warming experiment at the Harvard Forest site in Massachusetts (Melillo *et al*., 1995), soil warming of +5 ˚C resulted in a significant increase of carbon flux from the soils to atmosphere at the order of 56% (4000 kgC $ha^{-1}yr^{-1}$) for the first year of the experiment and 13% (900 kgC $ha^{-1}yr^{-1}$) for the second year of the experiment. Soil warming also results in a doubling of net nitrogen mineralization rate in the forest floor and mineral soils for the first and second years of the experiment (Melillo *et al*., 1995). The responses of NPP and carbon storage in our study are closely related to enhanced decomposition of soil organic matter, nitrogen availability in soils and plant nitrogen uptake, as the result of climate change.

Although the GFDL and MIT L-O climate models project a moderate increase of annual precipitation for doubled CO_2 globally (*i.e.*, +8.3% for GFDL and +11.5% for MIT L-O), the changes in precipitation made small contributions to the responses of NPP and carbon storage. The difference in global NPP responses between the scenario of complete climate change at 522 ppmv CO_2 and the scenario with no change in precipitation indicated that global NPP decreases 0.7% (0.34 PgC/yr) for the GFDL climate and 2.2% (1.10 PgC/yr) for the MIT L-O climate, because of lower precipitation (see Tables 2, 3). The results of this study showed that changes in temperature made a much larger contribution to the responses of NPP and carbon storage than changes in precipitation. In a simulation study that examines the response of NPP to climate change for 31 grassland sites worldwide, using the Century biogeochemistry model (Parton *et al*., 1995), changes in total plant production are shown to be more correlated to changes in temperature than to changes in precipitation.

Both the GFDL and MIT L-O climate models estimated a small change in cloudiness for doubled CO_2, *e.g.* a decrease in globally averaged annual mean cloudiness (–0.7% for GFDL and –2.6% for MIT L-O). Lower cloudiness results in higher total solar radiation and photosynthetically active radiation. Higher solar radiation may enhance water stress of plants through an increase in potential evapotranspiration, which may results in lower net primary production. The difference in global NPP responses between the scenario of complete climate change at 522 ppmv CO_2 and the scenario with no change in cloudiness indicated that global NPP increases 0.5% (0.24 PgC/yr) for the GFDL climate and 1.3% (0.62 PgC/yr) for the MIT L-O climate, because of higher cloudiness (see Tables 2, 3). Thus, a small change in cloudiness results in a small response of NPP and carbon storage of the terrestrial biosphere. The results are consistent with an earlier study that examined the effects of three alternative solar radiation data sets from the contemporary climate for the conterminous U.S. (Pan *et al*., 1996). In that study, solar radiation derived from the Cramer and Leemans climate database and the VEMAP project are 32% and 60% higher than the solar radiation derived from Hahn's cloudiness data, respectively. The estimates of annual NPP for the conterminous U.S. using solar radiation data from the Cramer and Leemans database and from the VEMAP project are about 8% and 10%

lower than the NPP estimate using solar radiation data derived from the Hahn's cloudiness data (Pan *et al*., 1996).

In addition to cloudiness, aerosols also influence the amount of solar radiation that reaches the earth's surface. Aerosols from the eruption of Mt. Pinatubo in June 14–15, 1991 reduced solar irradiance by 4% and decreased temperature by about 0.5 ˚C within the period of summer 1991 to summer 1992 (Blumthaler and Ambach, 1994). After the volcanic eruption of Mt. Pinatubo, the atmospheric CO_2 concentration began to drop in mid-1991 and decreased by 1.5 ppmv at Mauna Loa in May 1993 (Sarmiento, 1993). A large net sink of 2.5 PgC for this period, or 1.5 PgC/yr, is needed to account for the change in atmospheric CO_2 concentration, and the ^{13}C data seems to suggest that this carbon sink is mostly terrestrial (Sarmiento, 1993). Lower-than-normal temperatures may have caused net accumulation of carbon in a mature tropical rain forest in 1992–1993 (Grace *et al*., 1995). Given the sensitivity of carbon storage to a change in cloudiness, the reduction in solar radiation caused by the eruption may also result in a significant net terrestrial sink of carbon. However, the effects of aerosols was not included in the GFDL and 2-D MIT L-O climate models, and clouds are poorly represented in GCMs (Mitchell *et al*., 1989). Improving in projection of changes in cloudiness and aerosols by combined atmospheric chemistry models and GCMs will certainly be helpful in reducing uncertainty in responses of NPP and carbon storage to climate change.

VII.2 Effects of Interactions Among Changes in CO_2 and Climate Variables

In an earlier study on net primary production and carbon storage in the conterminous U.S. (VEMAP Members, 1995), TEM simulations indicated that the contributions from the interaction between climate change and elevated CO_2 to the continental NPP responses range from 8% in the OSU climate to 19% in the UKMO climate. Although their analysis indicates the importance of the interaction between a change in CO_2 and a change in climate, the relative role of a change in an individual climate variable and its interactions with changes in the other three driving variables was not quantified. However, the results presented in this paper show that interactions among changes in CO_2 level and climatic variables contribute significantly to the equilibrium responses of net primary production and carbon storage. Furthermore, the results suggest that the interaction between a change in CO_2 and a change in temperature is the most significant, given the magnitudes of changes in CO_2 and climate variables projected by the climate models.

In TEM, the interaction between elevated CO_2 and increased temperatures that influences NPP and carbon storage is caused by enhanced plant N uptake. As mentioned earlier, higher temperatures enhance decomposition of soil organic matter, resulting in decreases of soil carbon stocks. The rate of net nitrogen mineralization in soils increases with enhanced decomposition of soil organic matter. Mineralized nitrogen released from soil organic matter is assimilated by plants. Soil organic matter has low C/N ratio (10 – 20), while plant tissues have high C/N ratio (40 – 200). Thus, the shift of nitrogen from soils to vegetation allows substantial increase in vegetation carbon. Higher temperature also increases the rate of plant uptake of carbon (CO_2) and nitrogen (Raich *et al*., 1991). Therefore, for complete climate change at 522 ppmv CO_2, ecosystems are supplied with more mineralized nitrogen and carbon (CO_2) resources, which results in large increases in NPP and total carbon storage (vegetation carbon plus reactive soil organic carbon, *i.e.*, +137 PgC for the GFDL climate and +115 PgC for the MIT L-O climate).

Limited information is available on how the interactions among changes in CO_2 and climate variables affect the carbon and nitrogen cycles of the terrestrial ecosystem, as there are few factorial field experiments for whole ecosystems. In a field study for a tundra ecosystem, which used two levels of atmospheric CO_2 level (ambient CO_2, 680 ppmv CO_2) and temperature (ambient temperature, +4 ˚C temperature above ambient), the combination of elevated CO_2 and temperature increase resulted in an increase of net carbon storage that lasted for the three years of observation (Oechel and Riechers, 1986, 1987). The interactions among temperature, CO_2 and nutrient availability are key controlling factors in the responses of the tundra site (Melillo *et al*., 1990).

VIII. Future Studies

The analyses in this study are based on equilibrium or steady-state simulations of the TEM for potential natural vegetation. The results show that elevated CO_2 and temperature increases projected by the climate models play a major role in the equilibrium responses of primary production and carbon storage of the terrestrial biosphere. The responses of NPP and carbon storage to the projected changes in CO_2 and climate vary at the scales of the latitudinal bands and biomes. In addition, the results show that the interactions among changes in CO_2 and climate variables, especially the interaction between elevated CO_2 and temperature increase, may be important in the response of NPP and carbon storage. The relative role of the interaction between elevated CO_2 and climate change also varies by biome.

Our results also imply that the time courses of changes in atmospheric CO_2 concentration and climate are critical to the response of the terrestrial biosphere. In the next century, there is large uncertainty in anthropogenic emissions of CO_2 from fossil fuel combustion, which will result in different rates of change in atmospheric CO_2 concentration. Consequently, there are large uncertainties in the rate of climate change over time. The trajectory of changes in CO_2 and climate in the next century may have significant impacts on the structural and functional responses of the terrestrial biosphere. The large interannual variation in climate is one of several processes that account for the imbalance of the global carbon budget in the last few decades (Dai and Fung, 1993). In future studies, we will conduct transient simulations of TEM to track both the path and magnitude of the responses of NPP and carbon storage to changes in CO_2 and climate over time from the last century to the next century. Transient simulation of TEM will also allow us to incorporate the feedback of the terrestrial biosphere to the atmosphere (*e.g.*, net carbon flux between lands and atmosphere) in the studies of land-atmosphere interactions (Melillo, 1994) and integrated assessment of climate change (Prinn *et al*., 1996; Xiao *et al*., 1996).

Changes in land use also affect terrestrial carbon storage and the global carbon cycle (Houghton and Skole, 1990). As the results of this study are based on potential vegetation, we have not considered the direct effects of human activities on NPP and carbon storage of the terrestrial ecosystems. However, the results presented in this study provide a baseline for us to assess the effects of changes in land use and land cover on the terrestrial carbon budget in future studies.

As shown in the comparisons between the 3-D GFDL climate and 2-D MIT L-O climate, the relative role of the individual climate variables and the interactions among changes in CO_2 and climate variables to the overall response of NPP and carbon storage at larger spatial scales is affected by the geographical distributions of the projected changes in climate variables. There still are large uncertainties in the magnitudes and spatial distributions of changes of temperature, precipitation and cloudiness, as estimated by GCMs. Several climate modeling groups have begun to incorporate the effect of aerosols from anthropogenic sources on radiative forcing of climate for projections of future climate. Incorporation of the effect of aerosols into climate models would reduce the magnitude of temperature increases projected by climate models. Further improvement in climate models will reduce uncertainties in the magnitude and spatial distribution of climate change, and consequently uncertainties in responses of the terrestrial biosphere.

In a recent model comparison study (VEMAP Members, 1995), the estimates of the responses of NPP and carbon storage in the conterminous U.S. to climate change and elevated CO_2 differ among the three biogeochemistry models. Although TEM has indicated that the interaction between elevated CO_2 and climate change has an important effect on NPP and carbon storage, the results of the other models have indicated that this interaction is not important (VEMAP Members, 1995). Unfortunately, there is not enough information from field studies to confirm or deny the hypothesis that the interaction between elevated CO_2 and climate change has an important effect on NPP and carbon storage of the terrestrial ecosystems. Therefore, long-term partial or full factorial field experiments at the whole ecosystem level are critically needed to quantify interactions among key driving variables of the terrestrial ecosystems, which will provide important information for development and validation of ecosystem models.

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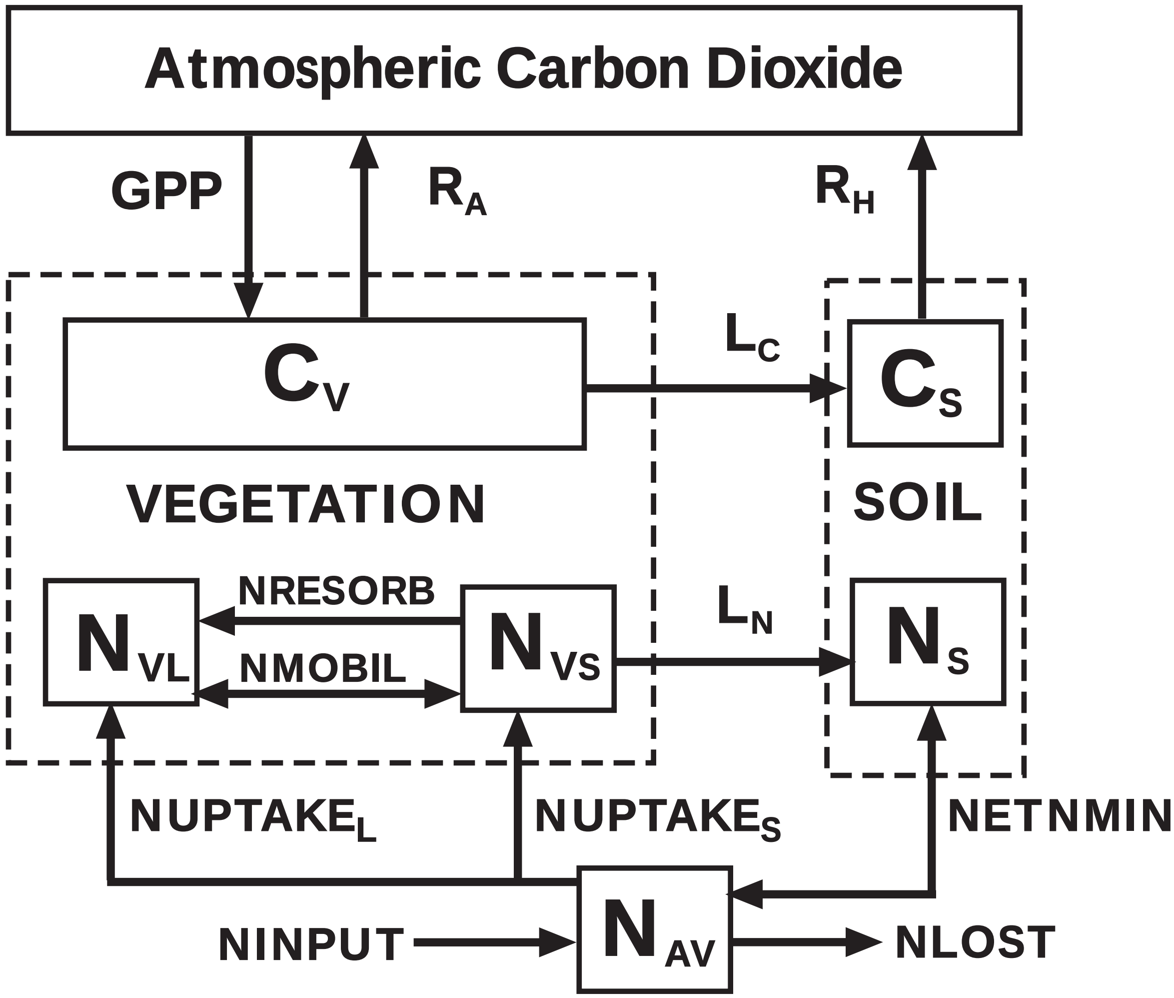

Figure 1. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in vegetation (C_V); structural nitrogen in vegetation (N_{VS}); labile nitrogen in vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic nitrogen in soils and detritus (N_S); and available soil inorganic 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.

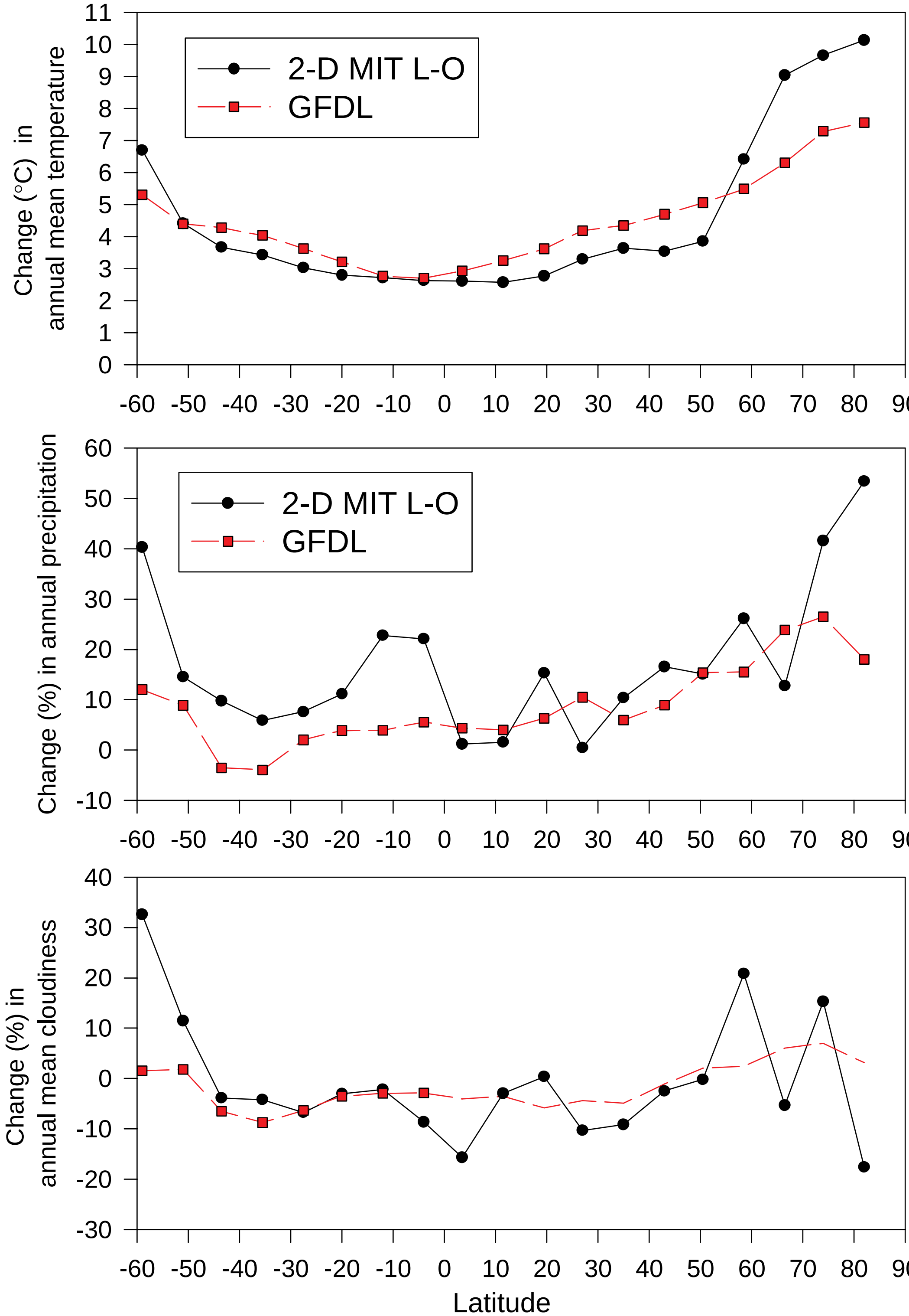

Figure 2. The zonal mean changes over land of annual mean temperature, annual precipitation and annual mean cloudiness between 1×CO2 and 2×CO2 simulations by the GFDL GCM and the 2-D MIT L-O climate model along the latitudinal bands as defined by the 2-D MIT L-O climate model. The outputs from the GFDL are averaged over the same latitudinal bands as those of the 2-D MIT L-O climate model.

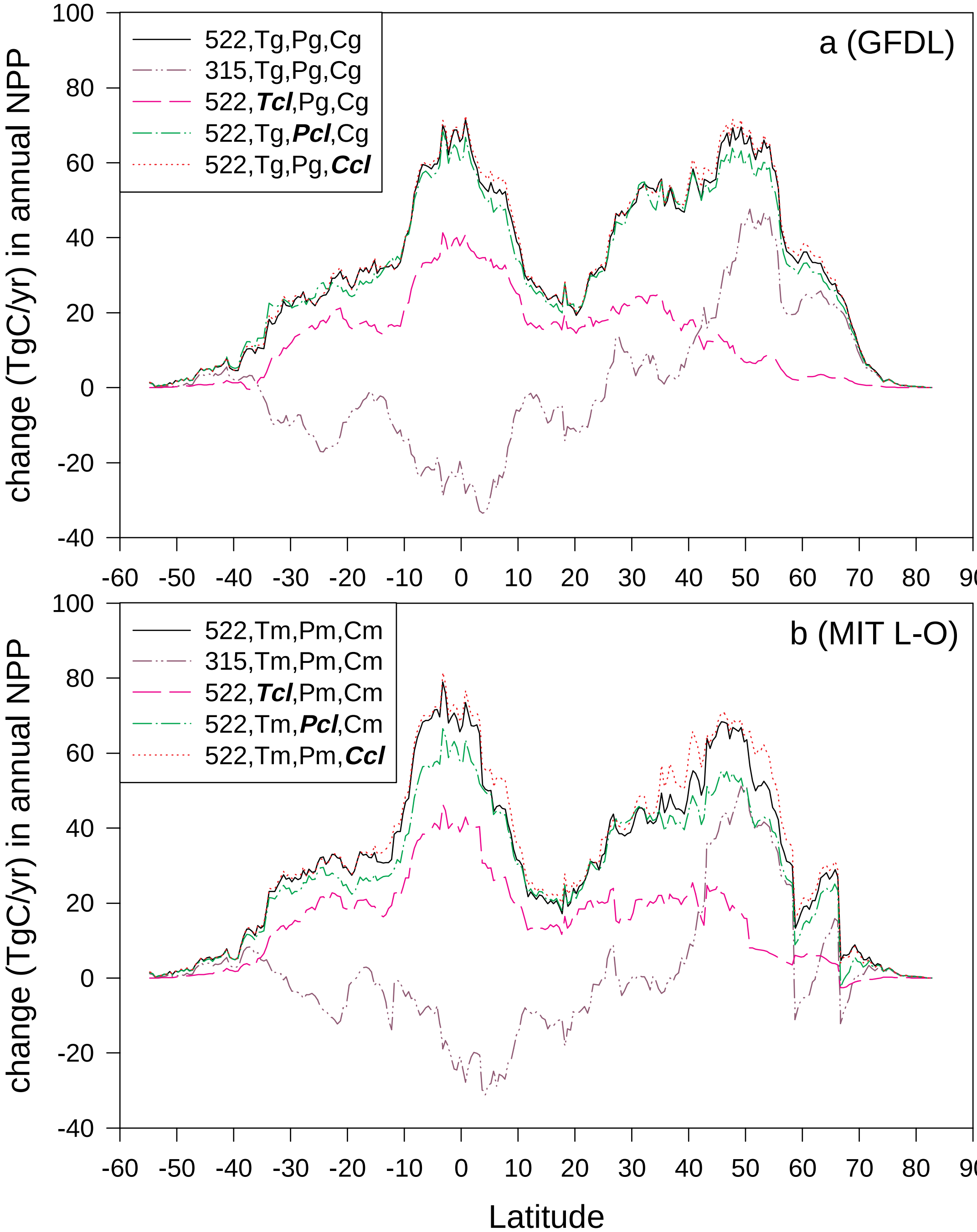

Figure 3. Latitudinal distributions of the responses of net primary production to change in atmospheric CO_2 concentration and changes in temperature, precipitation and cloudiness projected by the 3-D GFDL and 2-D MIT L-O climate models. The latitudinal bands have a 0.5° resolution. (a) GFDL climate; (b) MIT L-O climate.

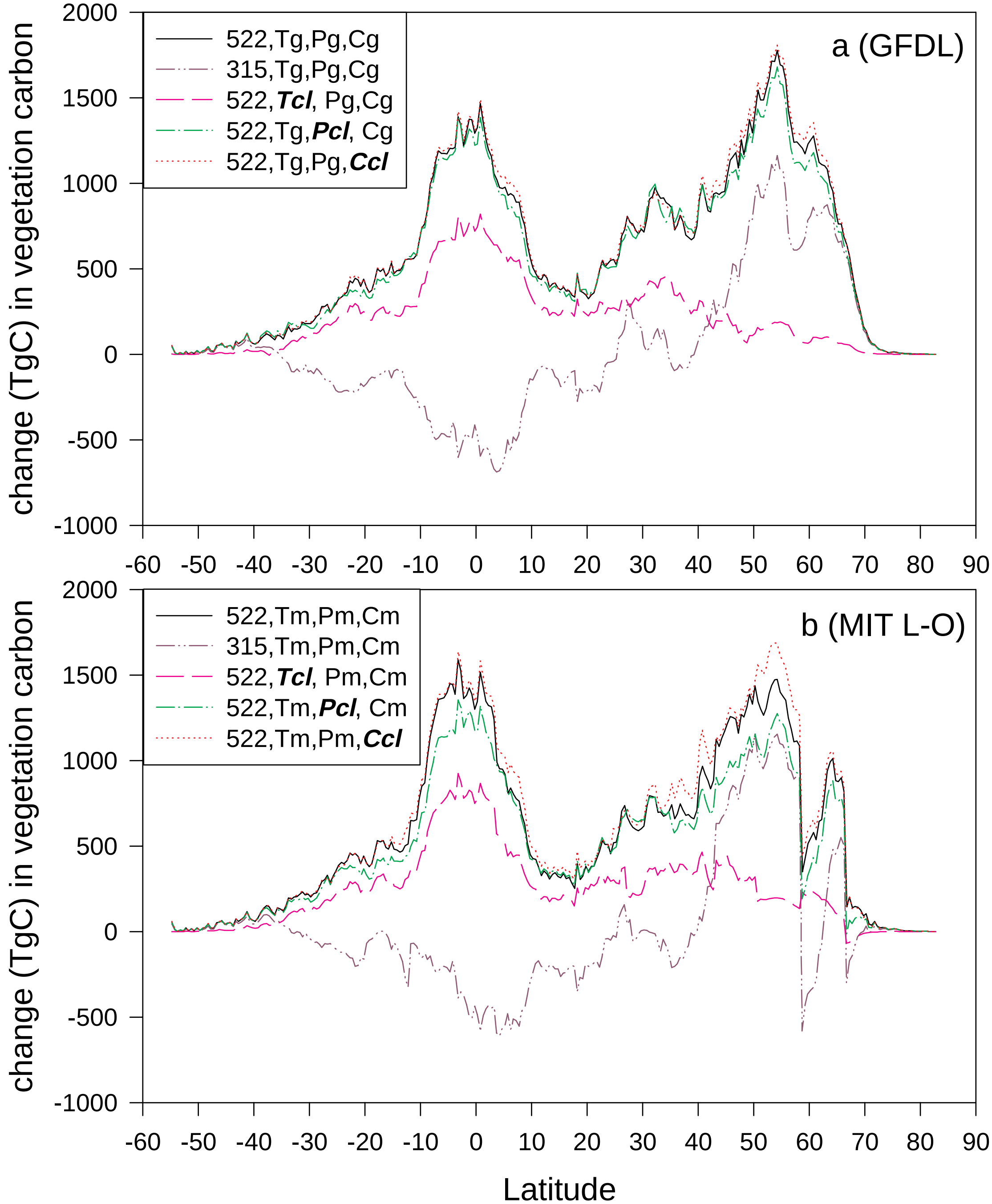

Figure 4. Latitudinal distributions of the responses of vegetation carbon to change in atmospheric CO_2 concentration and changes in temperature, precipitation and cloudiness projected by the 3-D GFDL and the 2-D MIT L-O climate models. The latitudinal bands have a 0.5˚ resolution. (a) GFDL climate; (b) MIT L-O climate.

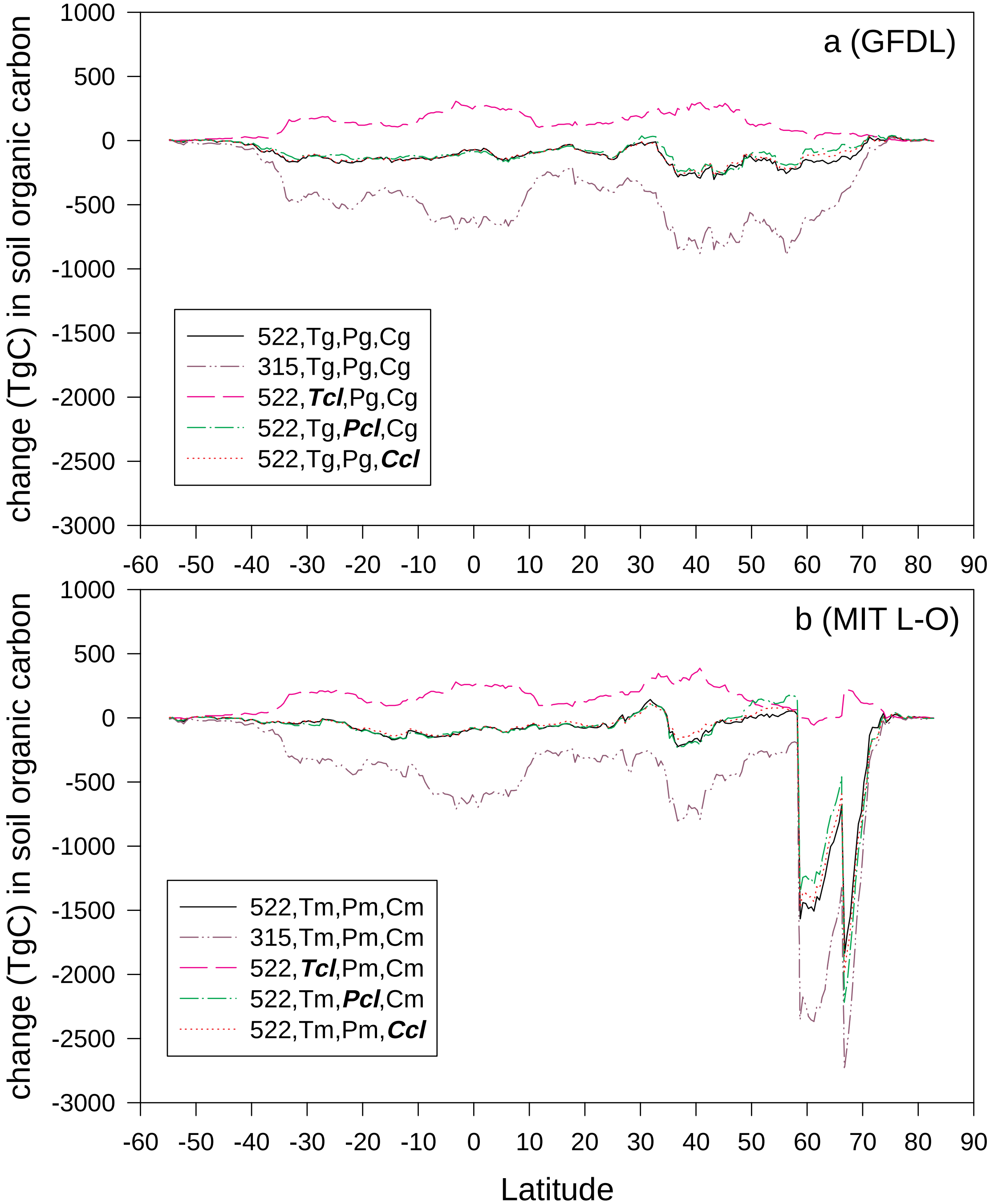

Figure 5. Latitudinal distributions of the responses of reactive soil organic carbon to change in atmospheric CO_2 concentration and changes in temperature, precipitation and cloudiness projected by the 3-D GFDL and 2-D MIT L-O climate models. The latitudinal bands have a 0.5˚ resolution. (a) GFDL climate; (b) MIT L-O climate.

Table 1. Design of the partial factorial experiment of TEM simulations.

Variable	baseline	CO_2 only	CO_2 & GFDL climate experiments					CO_2 & MIT L-O climate experiments				
			#1	#2	#3	#4	#5	#6	#7	#8	#9	#10
CO_2 (ppmv)	315	522	522	**315**	522	522	522	522	**315**	522	522	522
temperature	*Tcl*	*Tcl*	Tg	Tg	***Tcl***	Tg	Tg	Tm	Tm	***Tcl***	Tm	Tm
precipitation	*Pcl*	*Pcl*	Pg	Pg	Pg	***Pcl***	Pg	Pm	Pm	Pm	***Pcl***	Pm
cloudiness	*Ccl*	*Ccl*	Cg	Cg	Cg	Cg	***Ccl***	Cm	Cm	Cm	Cm	***Ccl***

Tcl, *Pcl*, *Ccl:* contemporary temperature, precipitation and cloudiness data from the Cramer & Leemans climate database; Tg, Pg, Cg: changes in temperature, precipitation and cloudiness projected by the GFDL GCM for doubled CO_2; Tm, Pm, Cm: changes in temperature, precipitation and cloudiness projected by the MIT L-O climate model for doubled CO_2.

Table 2. Estimates of net primary production for contemporary climate at 315 ppmv CO_2 and its equilibrium responses to elevated CO_2 and climate change projected by GFDL.

Table 3. Estimates of net primary production for contemporary climate at 315 ppmv CO_2 and its equilibrium responses to elevated CO_2 and climate change projected by MIT L-O.

Table 4. Estimates of for contemporary climate at 315 ppmv CO_2 and its equilibrium responses to elevated CO_2 and climate change projected by GFDL.

Table 5. Estimates of vegetation carbon for contemporary climate at 315 ppmv CO_2 and its equilibrium responses to elevated CO_2 and climate change projected by MIT L-O.

Table 6. Estimates of reactive soil organic carbon for contemporary climate at 315 ppmv CO_2 and its equilibrium responses to elevated CO_2 and climate change projected by GFDL.

Table 7. Estimates of reactive soil organic carbon for contemporary climate at 315 ppmv CO_2 and its equilibrium responses to elevated CO_2 and climate change projected by MIT L-O.