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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)

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Abstract Although there is a great deal of information concerning responses to increases in atmospheric CO_2 at the tissue and plant levels, there are substantially fewer studies that have investigated ecosystem-level responses in the context of integrated carbon, water, and nutrient cycles. Because our understanding of ecosystem responses to elevated CO_2 is incomplete, modeling is a tool that can be used to investigate the role of plant and soil interactions in the response of terrestrial ecosystems to elevated CO_2. In this study, we analyze the responses of net primary production (NPP) to doubled CO_2 from 355 to 710 ppmv among three biogeochemistry models in the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): BIOME-BGC (BioGeochemical Cycles), Century, and the Terrestrial Ecosystem Model (TEM). For the conterminous United States, doubled atmospheric CO_2 causes NPP to increase by 5% in Century, 8% in TEM, and 11% in BIOME-BGC. Multiple re-

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gression analyses between the NPP response to doubled CO_2 and the mean annual temperature and annual precipitation of biomes or grid cells indicate that there are negative relationships between precipitation and the response of NPP to doubled CO_2 for all three models. In contrast, there are different relationships between temperature and the response of NPP to doubled CO_2 for the three models: there is a negative relationship in the responses of BIOME-BGC, no relationship in the responses of Century, and a positive relationship in the responses of TEM. In BIOME-BGC, the NPP response to doubled CO_2 is controlled by the change in transpiration associated with reduced leaf conductance to water vapor. This change affects soil water, then leaf area development and, finally, NPP. In Century, the response of NPP to doubled CO_2 is controlled by changes in decomposition rates associated with increased soil moisture that results from reduced evapotranspiration. This change affects nitrogen availability for plants, which influences NPP. In TEM, the NPP response to doubled CO_2 is controlled by increased carboxylation which is modified by canopy conductance and the degree to which nitrogen constraints cause down-regulation of photosynthesis. The implementation of these different mechanisms has consequences for the spatial pattern of NPP responses, and represents, in part, conceptual uncertainty about controls over NPP responses. Progress in reducing these uncertainties requires research focused at the ecosystem level to understand how interactions between the carbon, nitrogen, and water cycles influence the response of NPP to elevated atmospheric CO_2.

Key words Global change · Carbon dioxide · Biogeochemistry · Net primary production (NPP) · Vegetation/Ecosystem Modeling and Analysis Project (VEMAP)

Introduction

During the past 250 years, the combustion of fossil fuels and deforestation have increased atmospheric carbon dioxide (CO_2) from preindustrial levels of approximately 280 ppmv to 358 ppmv in 1994 (IPCC WGI 1996). The IS92a projection of the Bern carbon cycle model is that CO_2 concentrations will reach approximately 450 ppmv by the year 2040 and 700 ppmv by the year 2100 (IPCC WGI 1996). These increases may have substantial effects on the global carbon cycle by influencing carbon assimilation and storage in terrestrial ecosystems (Melillo et al. 1996).

The effects of elevated CO_2 on carbon cycling have been experimentally investigated at the tissue, plant, and ecosystem levels (Strain and Cure 1994; McGuire et al. 1995a; Curtis 1996; Koch and Mooney 1996; Körner and Bazzaz 1996). Studies at the tissue level have focused primarily on the response of net photosynthesis and plant respiration. In contrast to studies at the tissue level, those at the level of the individual plant have focused primarily on the response of growth. Studies at the ecosystem level focus primarily on how growth responds to elevated CO_2 in the context of plant and soil interactions. Although there is a great deal of information concerning responses at the tissue and plant levels, substantially fewer studies have investigated ecosystem-level responses in the context of integrated carbon, water, and nutrient cycles. The experimental effort at the ecosystem level has lagged, in part because of the expense and complexity of investigating responses in the context of plant and soil interactions. Understanding derived from ecosystem-level studies is crucial if plant and soil interactions are important in the response of ecosystems to elevated CO_2. The experimental community studying CO_2 responses has substantially increased the effort at the ecosystem level in recent years (Drake et al. 1989, 1996; Curtis et al. 1990; Grulke et al. 1990; Mooney et al. 1991; Körner and Arnone, 1992; Norby et al. 1992, 1996; Oechel et al. 1993, 1996; Owensby et al. 1993, 1996, 1997; Zak et al. 1993, 1996; Kemp et al. 1994; Jackson et al. 1994; Rice et al. 1994; Arnone and Körner, 1995; Ellsworth et al. 1995; Cardon 1996; Day et al. 1996; Field et al. 1996, 1997; Hungate et al. 1996, 1997; Johnson et al. 1996; Bernston and Bazzaz, 1997; Franck et al. 1997; Körner et al. in press; Schortemeyer et al. in press; Stocker et al. 1997). Synthesis of the experimental effort at the ecosystem level is just beginning to emerge (e.g., Canadell et al. 1996; Koch and Mooney 1996). Because synthesis of experimental information at the ecosystem level is incomplete, modeling is a tool that can be used to investigate the role of plant and soil interactions in the response of terrestrial ecosystems to elevated CO_2.

Models are important tools in identifying potential ecosystem responses to global change because they are able to synthesize information in a quantitative fashion (Rastetter 1996). Ecologists are now developing whole-ecosystem models that consider responses to plant and soil CO_2 fertilization, and the more complex responses of ecosystems to simultaneous changes in climate and atmospheric CO_2 concentration. Different models conceptualize the role of interactions between plant and soil processes in different ways. The simulations of different models can be compared to explore the consequences of how different conceptualizations about plant and soil interactions influence the response of terrestrial ecosystems to elevated atmospheric CO_2. Thus, comparison of models has the potential to provide valuable insight that may be useful in designing experiments to elucidate controls over CO_2 responses at the ecosystem level.

The Vegetation/Ecosystem Modeling and Analysis Project (VEMAP; see VEMAP members 1995; Pan et al. 1996; Schimel et al. 1997) compared the responses of three biogeochemistry and three biogeography models to climate change and a doubling of atmospheric CO_2 for the conterminous United States. The biogeochemistry models, BIOME-BGC (Hunt and Running 1992; Running and Hunt 1993), Century (Parton et al. 1987, 1988, 1993), and TEM (Raich et al. 1991; McGuire et al. 1992, 1993, 1995b, 1997; Melillo et al. 1993, 1995), were driven by a common input database (Kittel et al. 1995, 1996). The three biogeochemistry models were run under different scenarios, combining a doubling of atmospheric CO_2 with climate changes projected by three general circulation models (GCMs), and vegetation maps produced by three biogeography models (BIOME2, MAPSS, and DOLY). When atmospheric CO_2 was doubled from 355 ppmv to 710 ppmv without climate change, equilibrium simulations among the three models projected an increase of net primary production (NPP) between 5% and 11% and an increase of carbon storage between 2% to 9% for the conterminous United States (VEMAP members 1995). Although each of these models represents interactions among the cycles of carbon, nitrogen, and water in ecosystems, interactions among the cycles are represented differently by the models (see VEMAP members 1995; Schimel et al. 1997). Because of the large number of responses in the factorial design of VEMAP (three biogeography models, three biogeochemistry models, three climate change scenarios, and two levels of atmospheric CO_2), we did not fully analyze the mechanisms responsible for the responses of the models to doubled atmospheric CO_2 in VEMAP members (1995).

In this study, we analyze in more detail the response of NPP to doubled CO_2 estimated by the three biogeochemistry models (BIOME-BGC, Century, and TEM) in VEMAP. To determine the doubled-CO_2 response, each biogeochemistry model was run to equilibrium at each CO_2 concentration for the potential vegetation (biomes) of each 0.5° grid cell (latitude × longitude) in the conterminous United States. In this analysis, we first review the continental-scale responses of NPP to doubled CO_2. We then evaluate the NPP responses of biomes and grid cells along climatic gradients of temperature and moisture to gain insight into the mechanisms controlling the CO_2 responses of the models. Finally, we analyze each model for the mechanisms that control the CO_2 responses of NPP across the spatial scope of the conterminous United States.

Patterns of NPP response along climatic gradients

Doubled atmospheric CO_2 causes simulated increases in NPP for the conterminous United States of 5% in Century, 8% in TEM, and 11% in BIOME-BGC (VEMAP members 1995). These increases are substantially lower than the 25–50% growth response to doubled CO_2 that has been observed in greenhouse studies that supply plants with sufficient nutrients and water (Kimball 1975; Gates 1985). As noted in VEMAP members (1995) and Schimel et al. (1997), these models all have optimal responses similar to those observed experimentally, which may be constrained by a number of modeled ecosystem processes. We examine patterns of NPP responses for biomes and grid cells along climatic gradients to understand the constraints that are operating in each of the models.

For BIOME-BGC, the NPP responses of biomes to doubled CO_2 range from increases of 4% in temperate deciduous savanna to 27% in alpine tundra (Table 1). Among the 17 biomes in the conterminous United States, the NPP response of BIOME-BGC is generally greater in cooler and drier biomes (Figs. 1a, b, 2a). An exception to the response pattern along climate gradients is subtropical arid shrubland, which is the hottest and driest biome, where NPP increases 20% in response to doubled CO_2 (Table 1). For Century, the NPP responses to doubled CO_2 range from 2% in cool temperate mixed forest to 10% in temperate mixed xeromorphic forest (Table 1). Among the biomes, re-

Table 1 Net primary production (NPP) responses to doubled atmospheric CO_2 (710 vs. 355 ppmv) simulated by the VEMAP biogeochemistry models

Biome	Temperature (°C)	Precipitation (mm)	NPP response (%)		
			BIOME-BGC	Century	TEM
Tundra	−0.5	788.2	27.29	7.83	4.73
Boreal conifer forest	0.6	733.1	6.05	3.37	3.50
Maritime conifer forest	7.2	1505.9	10.09	4.10	7.59
Continental conifer forest	3.4	666.9	15.97	4.51	4.12
Cool temperate mixed forest	5.4	1016.4	12.74	1.88	3.08
Warm temperate/subtropic mixed forest	16.5	1296.2	6.69	2.25	11.82
Temperate deciduous forest	11.0	1102.9	15.50	4.16	8.19
Temperate mixed xeromophic forest	12.4	518.7	10.94	10.00	21.22
Temperate conifer xeromophic forest	8.2	356.6	22.59	4.95	23.31
Temperate deciduous savanna	12.3	903.5	4.11	6.45	8.25
Warm temperate subtropic mixed savanna	17.2	677.8	5.12	5.21	12.65
Temperate conifer savanna	4.2	417.5	26.20	7.99	5.71
C3 grasslands	6.6	450.1	22.44	9.85	1.25
C4 grasslands	11.1	597.9	4.78	9.89	2.97
Mediterranean shrublands	11.8	528.8	8.74	7.68	19.25
Temperate arid shrublands	6.2	355.7	23.74	6.50	15.12
Subtropical arid shrublands	16.9	277.8	19.64	2.23	26.33

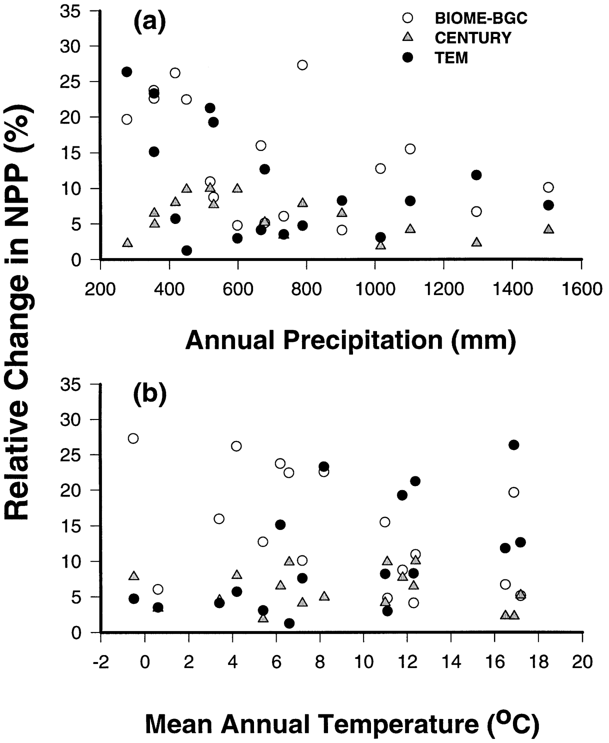

Fig. 1 Relative net primary production (*NPP*) responses (%) of biomes in the conterminous USA to doubled atmospheric CO_2 (355 to 710 ppmv) vs. biome annual precipitation (**a**) and biome mean annual temperature (**b**) as simulated by the VEMAP biogeochemistry models BIOME-BGC, Century, and TEM

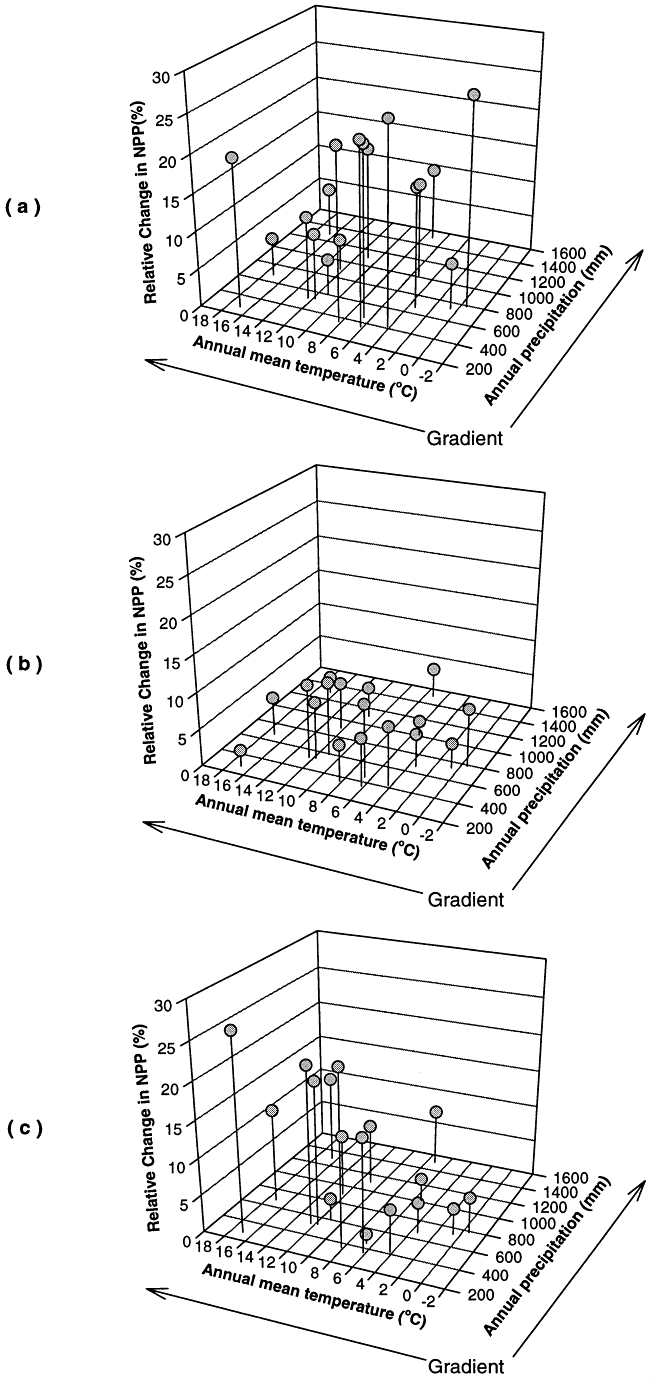

Fig. 2 Relative NPP responses (%) of biomes in the conterminous USA to doubled atmospheric CO_2 (355 to 710 ppmv) vs. biome annual precipitation and biome mean annual temperature as simulated by the VEMAP biogeochemistry models BIOME-BGC (**a**), Century (**b**), and TEM (**c**)

sponses are greatest in semi-arid systems where annual precipitation ranges between 400 and 600 mm (e.g., grasslands and mixed xeromorphic forest; Figs. 1a, 2b). The response of NPP has no relationship with temperature (Figs. 1b, 2b). For TEM, the NPP response to doubled CO_2 ranges from 1% in C3 grassland to 26% in subtropical arid shrublands (Table 1). Among the biomes, responses are greater in warmer and drier biomes (e.g., subtropical and temperate arid shrublands; Figs. 1a, b, 2c).

A multiple regression between the NPP response of biomes to doubled CO_2 and the mean annual temperature and annual precipitation of biomes indicates that there is a tendency for a negative relationship between the response of NPP and precipitation for all three models (Table 2). In contrast, there are different relationships between the response of NPP and temperature for the three models. There is a negative relationship in the responses of BIOME-BGC, a positive relationship in the responses of TEM, and no relationship in the responses of Century.

At the grid cell level, the relationships between the NPP response to doubled CO_2 and the mean annual temperature and annual precipitation are similar to the biome-level relationships (Table 2). The models disagree on the relationship of NPP response with temperature. A negative relationship exists between NPP response and precipitation for all three models with the slopes for BIOME-BGC and TEM about twice that of Century. Although the NPP responses of BIOME-BGC and TEM are more sensitive to spatial variability in precipitation, little of the grid cell variation in NPP response is explained by the multiple regressions (Table 2).

Table 2 Multiple regression analysis of the relative NPP response (%) of biomes ($n = 17$) and grid cells ($n = 3168$) to doubled CO_2: relationship with the mean annual temperature and annual precipitation

Model	Coefficients			*P*-value		R^2
	Constant	Precipitation	Temperature	Precipitation	Temperature	
Biomes						
BIOME-BGC	27.50	−0.0101	−0.681	0.051	0.042	0.414
Century	8.75	−0.0034	−0.055	0.089	0.655	0.204
TEM	9.80	−0.0094	+0.845	0.046	0.009	0.496
Grid cells						
BIOME-BGC	26.50	−0.0077	−0.619	<0.0001	<0.0001	0.153
Century	8.50	−0.0035	−0.012	<0.0001	<0.2371	0.174
TEM	4.94	−0.0066	+0.869	<0.0001	<0.0001	0.334

To understand the reasons for similarities and differences in NPP responses among the models, we analyze the mechanisms responsible for the responses of NPP. The strategy for this analysis is to examine how elevated CO_2 concentration will influence the formulations of processes in each model, and how feedbacks associated with the water and nitrogen cycles ultimately influence the response of carbon assimilation. First, for the model under analysis we present overviews of the formulations for carbon assimilation and other relevant processes. We then analyze the effects of CO_2 that appear to be insensitive to climate in their influence on parameters or formulations of the model. Finally, we analyze the effects of CO_2 that are sensitive to climate to gain insight into how interactions of the carbon, water, and nitrogen cycles represented by the model influence the response of carbon assimilation to elevated CO_2.

Mechanisms that control CO_2 responses of NPP in BIOME-BGC

Overview of canopy carbon assimilation

Canopy carbon assimilation in BIOME-BGC is expressed as:

$$\mathrm{PSN} = \mathrm{f}(A_{\max}(G, \mathrm{TS}, [LN], [\mathrm{CO}_{2:\mathrm{i}}]), \alpha, \mathrm{LAI}, \mathrm{PAR}, T) \qquad (1)$$

where $A_{\max}$ is a function representing maximum rate of photosynthetic CO_2 uptake, G is canopy conductance to water vapor, TS is transpiration based on the Penman-Monteith formulation, [LN] is leaf nitrogen concentration, $[CO_{2:i}]$ is the concentration of intercellular CO_2, α is the photosynthetic efficiency (CO_2 fixed per photon absorbed), LAI is the leaf area index of the canopy, PAR is photosynthetically active radiation, and T is air temperature. The biochemistry of the C3 photosynthetic pathway in BIOME-BGC is represented by $A_{\max}$, a Michaelis-Menton function (Farquhar et al. 1980; Leuning 1990) that simulates the rate of carbon assimilation at maximum photosynthetic photon flux density (ppfd), optimum temperature, leaf nitrogen concentration ([LN]), canopy conductance (G), and intercellular CO_2 concentration ($[CO_{2:i}]$). Intercellular CO_2 concentrations are linearly related to atmospheric CO_2. The components in Eq. 1 are expressed as:

$$G = \mathrm{f}([\mathrm{CO}_{2:\mathrm{a}}], \mathrm{LAI}, \mathrm{LWP}, \mathrm{VPD}, T) \qquad (1a)$$

$$\mathrm{LWP} = 0.2[1/(\mathrm{SWP})] \qquad (1b)$$

$$\mathrm{SWP} = \mathrm{SWC}/\mathrm{MAXH_2O} \qquad (1c)$$

$$\mathrm{TS} = \mathrm{f}(\mathrm{LAI}, T, \mathrm{VPD}, \mathrm{PAR}, G) \qquad (1d)$$

$$\alpha = \mathrm{f}([\mathrm{CO}_{2:\mathrm{a}}], [\mathrm{CO}_{2:\mathrm{i}}], \mathrm{LAI}, T) \qquad (1e)$$

where $[CO_{2:a}]$ is concentration of atmospheric CO_2, LWP is the leaf water potential, VPD is vapor pressure deficit, SWP is the soil water potential, SWC is the soil water content, and $MAXH_2O$ is the maximum water-holding capacity (Running and Coughlan 1988; VEMAP members 1995).

In BIOME-BGC, NPP is half of the carbon assimilated by the canopy. The doubled-CO_2 response of NPP is influenced by a number of variables and processes in the canopy carbon assimilation model of BIOME-BGC that are sensitive to increases in atmospheric CO_2 (Table 3). We first examine responses that are insensitive to climate and then examine those that are sensitive to climate.

CO_2 responses not influenced by climatic gradients

In BIOME-BGC, the doubled-CO_2 responses of intercellular CO_2, canopy conductance, and leaf nitrogen concentration are prescribed and do not influence the response of NPP along climatic gradients. Intercellular CO_2 increases with a rise in atmospheric CO_2 because these two quantities are linearly related in the model. The observation that leaf-level stomatal conductance is reduced by elevated CO_2 is represented in BIOME-BGC by prescribing an ~20% reduction in canopy conductance for a doubling of atmospheric CO_2. Similarly, BIOME-BGC represents the observation that elevated CO_2 reduces leaf nitrogen concentration by prescribing a 40% reduction in conifers, 30% reduction in broadleaf forests and shrublands, and a 20% reduction in C3

Table 3 List of parameters, variables, and processes influenced by doubled atmospheric CO_2 for each of the VEMAP biogeochemistry models

BIOME-BGC	Century	TEM
1. Intercellular CO_2 increase with doubled atmospheric CO_2	1. Effect of atmospheric CO_2 on potential production rate increases with doubled atmospheric CO_2	1. Intercellular CO_2 increases with doubled atmospheric CO_2
2. Prescribed 20% reduction in canopy conductance	2. Prescribed 20% reduction in transpiration	2. The amount of the increase in intercellular CO_2 concentration varies with canopy conductance
3. Prescribed 20 ~ 40% reduction in leaf nitrogen concentration.	3. Soil moisture increases with the prescribed reduction in transpiration	3. Potential production increases with the increase of intercellular CO_2
4. Photosynthesic efficiency (α) increases with doubled atmospheric CO_2	4. Prescribed 20% increase in C:N ratio of foliage	4. Nitrogen constraints on the construction of new tissue cause down-regulation of photosynthesis
5. Transpiration is reduced with the prescribed reduction in canopy conductance	5. Decomposition rate decreases with the lower N concentration in litterfall	5. The degree of down-regulation depends on soil moisture, air temperature, amount of carbon in the vegetation, and the amounts of soil inorganic nitrogen and vegetation-labile nitrogen
6. Soil moisture increases with the reduction in transpiration	6. Effect of water on decomposition increases with the increase in soil moisture	
7. Leaf water stress decreases with the increase in soil moisture	7. Nitrogen availability for plant increases with the increase in decomposition	

grasses for a doubling of atmospheric CO_2. Thus, carbon assimilation increases as intercellular CO_2 increases, and decreases as canopy conductance and leaf nitrogen concentration decrease.

CO_2 responses influenced by climatic gradients

Temperature

Responses of photosynthetic efficiency and transpiration are sensitive to temperature. Because photosynthetic efficiency decreases with increasing temperature, the relative doubled-CO_2 response of NPP is sensitive to temperature (McMurtrie et al. 1992). Although NPP is sensitive to the temperature sensitivity of photosynthetic efficiency, the effect in BIOME-BGC is small (Hunt and Running 1992).

Although the doubled-CO_2 changes in canopy conductance do not directly influence the relative response of NPP along climatic gradients, changes in canopy conductance influence transpiration, which is sensitive to climate. Decreases in canopy conductance reduce leaf-level transpiration, which increases soil water and leaf water potential to increase leaf area index (Running and Gower 1991). Thus, reductions in leaf-level transpiration will enhance the response of NPP. We analytically evaluate the sensitivity of the doubled-CO_2 response of transpiration along climatic gradients to understand the climatic sensitivity of NPP responses to doubled CO_2.

In BIOME-BGC, transpiration (TS) is represented by the Penman-Monteith equation, and is expressed as:

$$\mathrm{TS} = \frac{\mathrm{SLOPE\ RAD} + (\mathrm{CP\ PA})\mathrm{VPD}/\mathrm{RA}}{\mathrm{SLOPE}\ +\ \mathrm{GAMMA}\{1 + 1/(G\ \mathrm{RA})\}}\left(\frac{\mathrm{DAYL}}{\mathrm{LE}\ 1000}\right) \quad (2)$$

where TS is canopy transpiration ($m^3\ day^{-1}$); SLOPE is the derivative of humidity deficit (mbar $°C^{-1}$) at ambient air temperature (T); RAD is average canopy net radiation ($W\ m^{-2}$); CP is specific heat of air ($J\ kg^{-1}\ °C^{-1}$); PA is density of air ($kg\ m^{-3}$); VPD is vapor pressure deficit from canopy to air (mbar); RA is canopy aerodynamic resistance, which is fixed at $1.0\ s\ m^{-1}$ for trees and shrubs, and $0.01\ s\ m^{-1}$ for all grasses; G is leaf conductance ($s\ m^{-1}$); GAMMA is the psychometric constant (mbar $°C^{-1}$); LE is latent heat of vaporization of water ($J\ kg^{-1}$); and DAYL is day-length ($s\ day^{-1}$). Fundamental components of the Penman-Monteith TS formulation include absolute humidity deficit (VPD) and the derivative of humidity deficit with temperature (SLOPE), which are directly controlled by average daily air temperature (T) and relative humidity. We simplify Eq. 2 by replacing terms that do not depend on temperature and moisture with constants (m_x) (see Appendix), and express the absolute change in leaf-level transpiration to doubled CO_2 as:

$$\Delta\mathrm{TS} = -0.25 \frac{m_4\, m_5(m_1\ \mathrm{SLOPE} + m_2\ \mathrm{VPD})/G_{1\times CO_2}}{(\mathrm{SLOPE} + m_3 + 1.25\, m_4/G_{1\times CO_2})(\mathrm{SLOPE} + m_3 + m_4/\ G_{1\times CO_2})} \quad (3)$$

where $G_{1\times CO_2}$ is canopy conductance at $1 \times CO_2$. Equation 3 indicates that canopy transpiration is potentially reduced at doubled CO_2, (i.e., ΔTS is negative) when a prescribed reduction in canopy conductance is implemented in association with doubled CO_2. Because VPD and SLOPE increase with temperature (see Appendix), the relative reduction in transpiration monotonically decreases with increasing temperature (see Fig. 3a).

Moisture

To evaluate the moisture sensitivity of the doubled-CO_2 response of transpiration, we further simplify Eq. 3 so that it does not depend on temperature-sensitive variables (see Appendix):

$$\Delta TS = -0.25 \frac{m_6}{\frac{(m_7\, G_{1\times CO_2})^2 + 1.25\,(m_4)^2}{G_{1\times CO_2}} + 2.25\, m_4\, m_7} \qquad (4)$$

By differentiating Eq. 4 with respect to G, we determine that the maximum reduction in transpiration occurs when canopy conductance equals 0.000174 m s^{-1} at 10°C temperature (see Appendix). Because canopy conductance is related to soil moisture (SWC) through soil water potential and leaf water potential (see Eq. 1a–c), we are able to determine that the relationship between the reduction in transpiration and soil moisture is optimized when soil moisture equals 30.8 mm (see Appendix and Fig. 3b). For different temperatures, the relationship is similar to that in Fig. 3b. Thus, the largest potential reduction in transpiration associated with doubled CO_2 occurs when soils are substantially dry, but not extremely dry. Because reductions in transpiration translate into increases in leaf area (see Appendix), the greatest relative increases in NPP tend to be associated with the largest potential reduction in transpiration.

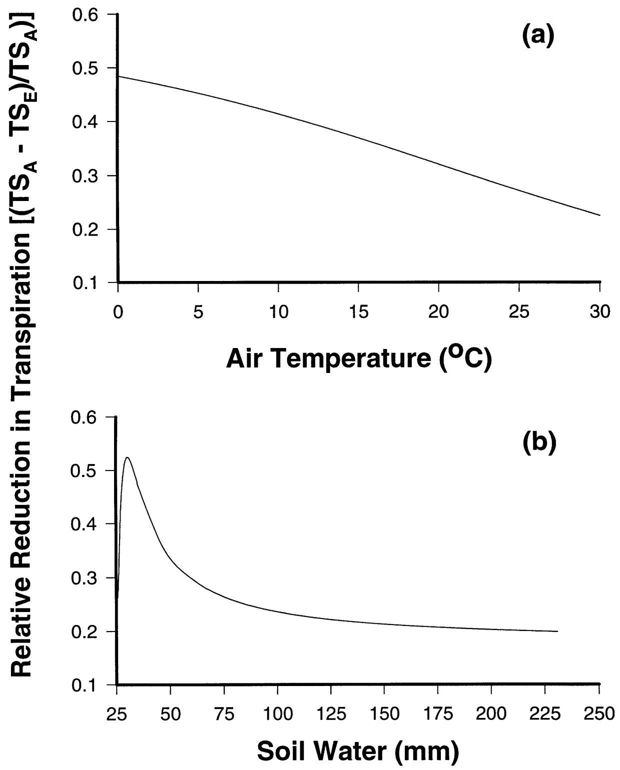

Fig. 3 The relative reduction in transpiration (TS) for BIOME-BGC associated with a doubled atmospheric CO_2 along gradients of air temperature (**a**) and soil moisture (**b**). Relative reduction in transpiration is calculated as $(TS_A - TS_E)/TS_A$ where TS_A is transpiration at ambient atmospheric CO_2 and TS_E is transpiration at doubled (elevated) CO_2

Mechanisms that control CO_2 responses of NPP in Century

Overview of plant carbon assimilation

The equation of potential NPP (NPP_p) in Century is expressed as:

$$NPP_P = NPP_{max}\, T_p M_p S_p\, ACO_2 \qquad (5)$$

where NPP_{max} is a biophysically defined maximum NPP, T_p is the effect of temperature on NPP, M_p the effect of soil moisture, S_p the effect of self-shading, and ACO_2 is the effect of atmospheric CO_2. The functional forms for T_p, M_p, and S_p are given in Parton et al. (1993).

To determine when NPP_P is constrained by nutrient availability, a nutrient-limited NPP (NPP_N) is calculated to estimate the fraction of NPP_P that can be achieved while maintaining appropriate tissue C:N stoichiometry:

$$NPP_N = \sum [(\text{Navail Rtimp} + \text{Ninput})\, F_i]\, \text{C:N}_i \qquad (6)$$
$$i = 1 \text{ to } n$$

where n is the number of plant pools. The term Navail is the available mineral N in the soil solution plus N in plant storage pools; plant storage results from N that is resorbed from senescent foliage and is available for new growth in the spring, or following drought in perennial vegetation. The term Rtimp is a weighting factor for plant nutrient uptake based on root biomass; Rtimp is 1 at an upper threshold of biomass and 0 if root biomass is zero. The term Ninput is the N available from fixation and deposition. The terms F_i and C:N$_i$ are the fraction of total N uptake (Navail Rtimp + Ninput) allocated to plant part i, and the C:N ratio of plant part i, respectively; plant parts include roots, leaves, and fine and coarse wood. In Century, allocation between plant pools and C:N ratios of plant pools are specified for each vegetation type (Schimel et al. 1994; VEMAP members 1995) based on observations at sites used to parameterize the model.

The final calculation of NPP is defined by:

$$NPP = \min(NPP_N, NPP_P) \qquad (7)$$

Although NPP_N is nearly always less than NPP_P, if NPP_P increases, NPP will generally follow because the floating C:N ratios are based on a linear N supply/demand equation until the lower critical C:N threshold is reached (see Parton et al. 1993). Experimental evidence supports floating C:N ratios between years (Schimel et al. 1991). If N availability goes up (e.g., if N mineralization increases because of warmer or wetter soils: Schimel et al. 1994), NPP will increase as NPP_N approaches NPP_P.

The doubled-CO_2 response of NPP is influenced by a number of variables and processes in Century that are sensitive to increases in atmospheric CO_2 (Table 3). We first examine responses that are insensitive to climate and then examine those that are sensitive to climate.

Overview of decomposition

In Century, decomposition for surface and soil structural material is calculated as:

$$\frac{dC_i}{dt} = K_i \, Lc \, f(T) \, f(M) \, C_i \qquad (8)$$

and for active soil organic matter (SOM) as:

$$\frac{dC_i}{dt} = K_i \, f(T) \, f(M) \, Tm \, C_i \qquad (9)$$

where C_i is the amount of carbon in a particular soil carbon pool, K_i is the maximum decomposition rate, Lc is the impact of lignin content on decomposition of structural organic matter, f(*T*) is the effect of soil temperature on decomposition (Fig. 4a), f(*M*) is the effect of soil moisture on decomposition (Fig. 4b), and Tm is the effect of soil texture on SOM turnover. The maximum decomposition rate (K_i) varies for each pool of soil organic matter.

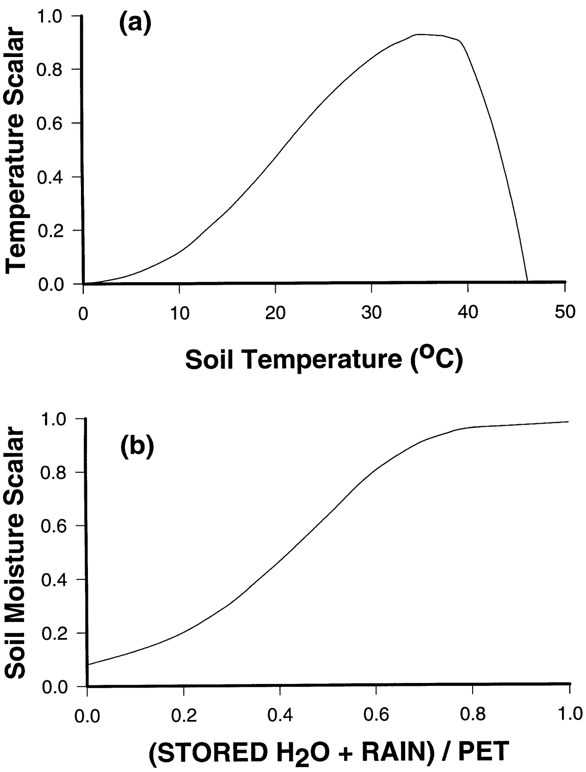

Fig. 4 The scalar functions in the Century decomposition formulation for the effects of soil temperature (**a**) and soil moisture (**b**) on decomposition

CO_2 responses not influenced by climatic gradients

In Century, the doubled-CO_2 responses of ACO_2 in Eq. 5, C:N in Eq. 6, and transpiration in the water balance model are prescribed and do not directly influence the pattern of NPP along climatic gradients. The variable ACO_2 monotonically increases according to a nonlinear relationship relative to the baseline CO_2 level:

$$ACO_2 = 1 + \frac{CO_2eff - 1}{\log_{10}(2.0)} \log_{10}\left(\frac{CO_2conc}{CO_2bas}\right) \qquad (10)$$

where the CO_2eff is the potential effect of increasing CO_2 concentrations above the baseline, CO_2conc is the elevated concentration of CO_2, and CO_2bas is the baseline concentration of CO_2. Because the parameter CO_2eff is 1.2, ACO_2 will increase 20% with a doubling of atmospheric CO_2. Thus, the multiplicative effect of ACO_2 in Eq. 5 will enhance NPP_P by 20% for a doubling of atmospheric CO_2.

In Century, the C:N ratios of leaf biomass are increased by 20% with a doubling of atmospheric CO_2, which causes NPP_N to increase by 20% for no change in Navail. Because doubled CO_2 levels tend to increase both NPP_N, through the response of C:N ratios, and NPP_P, through the response of ACO2, by 20%, the prescribed reduction in leaf nitrogen concentration results in lower litter quality, which tends to decrease decomposition rates and Navail (Parton et al. 1995). Elevated CO_2 does not influence the effect of soil temperature on decomposition (Fig. 4a).

In Century, doubled atmospheric CO_2 causes a prescribed 20% decrease in transpiration per unit leaf mass. By modifying the available water in the soil, the change in transpiration rate influences M_p in Eq. 5. The function M_p is linearly expressed as:

$$M_p = a(\text{rainfall} + \text{stored } H_2O)/PET - b \qquad (11)$$

where coefficients *a* and *b* depend on soil texture. On first inspection, elevated CO_2 will tend to increase M_p because reduced transpiration translates into an increase in soil moisture. However, increased soil moisture enhances leaf area, which partially compensates for the reduced transpiration per unit leaf mass. Changes in M_p associated with reduced transpiration have the potential to differentially influence decomposition along moisture gradients.

CO_2 responses influenced by climatic gradients

In Century, the effect of soil moisture on decomposition increases monotonically with soil moisture (Fig. 4b). Because the prescribed reduction of transpiration in Century tends to increase soil moisture, the response of decomposition to doubled CO_2 is relatively higher with increasing 1 × CO_2 soil moisture (Fig. 5a). By taking the ratio of the 1 × CO_2 and 2 × CO_2 decomposition responses in Fig. 5a, the relative response of decomposition tends to be greater in semi-arid regions where the

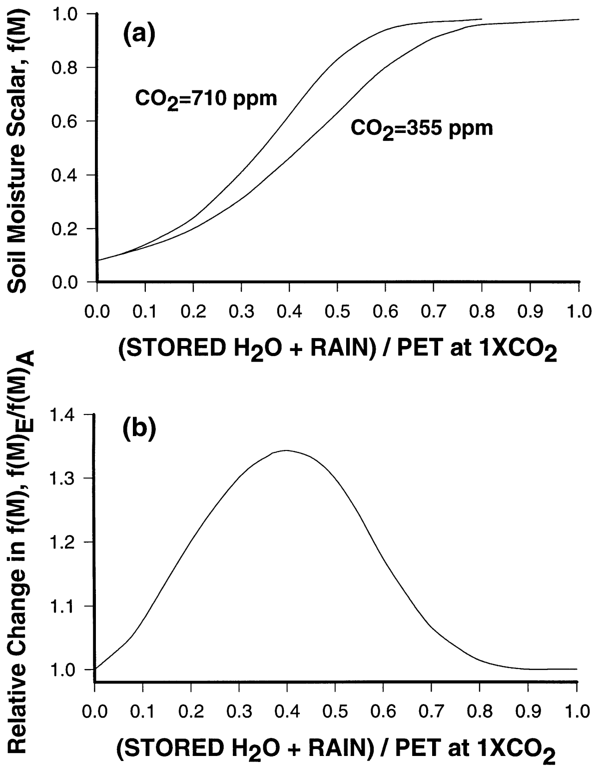

Fig. 5 a The ambient-CO_2 (355 ppmv) and doubled-CO_2 (710 ppmv) scalar functions in the Century decomposition formulation for the effect of soil moisture on decomposition, f(*M*), vs. soil moisture levels at ambient atmospheric CO_2 (1 × CO_2); relative to the soil moisture level at ambient CO_2, the reduction of transpiration effectively shifts the scalar function to the left. **b** The ratio of the doubled-(elevated) CO_2 scalar function, $f(M)_E$, to the ambient scalar function, $f(M)_A$, for the effects of soil moisture on decomposition in Century vs. soil moisture levels at ambient atmospheric CO_2 (1 × CO_2)

ratio of precipitation plus stored soil water to PET is approximately equal to 0.4 (Fig. 5b). Because the relative response of decomposition in Fig. 5b tends to cause greater relative responses of nitrogen availability in semi-arid regions, the responses of NPP to elevated CO_2 tend to be greater in semi-arid regions (Figs. 1, 2b).

Mechanisms that control CO_2 responses of NPP in TEM

Overview of plant carbon assimilation

Carbon assimilation in TEM is represented by gross primary production (GPP), which is expressed as:

$$\mathrm{GPP} = \mathrm{C}_{\max}\ \mathrm{f(PAR)}\ \mathrm{f(LEAF)}\ \mathrm{f}(T)\mathrm{f}(\mathrm{C_a}, G_\mathrm{V})\ \mathrm{f(NA)} \tag{12}$$

where C_{max} is the maximum rate of C assimilation, PAR is the photosynthetically active radiation, LEAF is leaf area relative to the maximum annual leaf area, *T* is the monthly air temperature, C_a is the atmospheric concentration of carbon dioxide, G_V is relative canopy conductance, and NA is nitrogen availability. NPP is calculated as the difference between GPP and plant respiration. A doubling of CO_2 directly influences f(C_a, G_V) and influences f(NA) through feedbacks of the nitrogen cycle that influence GPP (Table 3).

CO_2 responses not influenced by climatic gradients

In TEM, the term f(C_a, G_V) is described by the hyperbolic (Michaelis-Menton) function:

$$\mathrm{f}(\mathrm{C_a}, G_\mathrm{V}) = \mathrm{C_i}/(\mathrm{C_i} + \mathrm{k_c}) \tag{13}$$

where C_i represents the intercellular concentration of CO_2 in the canopy and k_c is the half-saturation constant for CO_2 uptake. Similar to BIOME-BGC, C_i increases linearly with C_a. In TEM, this dependence is described by $G_V \times C_a$ (see Raich et al. 1991). Similar to the response of leaf area in BIOME-BGC to potential reductions in transpiration, TEM implicitly assumes that the allocation of leaf area to carbon uptake responds so that overall canopy conductance and actual evapotranspiration (AET) do not change in response to elevated CO_2. Although leaf area is assumed to change, the effect of relative leaf area on GPP, f(LEAF), is not affected by elevated CO_2. This assumption is based on the hypothesis that increases in leaf area will offset decreases in transpiration per unit leaf area (see Eamus and Jarvis 1989). The half-saturation constant k_c 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 with G_V equal to 1, i.e., f(680, 1)/f(340, 1) = 1.37. When relative canopy conductance (G_V) is a constant, the function f(C_a, G_V) monotonically increases according to a hyperbolic relationship with elevated atmospheric CO_2 (Fig. 6a). Although GPP is potentially enhanced by 37% in response to doubled atmospheric CO_2 for no water or nitrogen limitation, the actual response along climatic gradients depends on both water and nitrogen availability.

CO_2 responses influenced by climatic gradients

The effects of moisture availability on CO_2 response are implemented through Eq. 13, where relative canopy conductance, G_V, increases monotonically with the ratio AET and PET (see Appendix). Because the intercellular CO_2 concentration depends on both canopy conductance and atmospheric CO_2 ($G_V \times C_a$), the effect of moisture availability on canopy conductance influences the potential response of GPP to elevated atmospheric CO_2. Under conditions of very low moisture availability, GPP may increase by more than 90% if nitrogen availability does not limit production (Fig. 6b). Thus, the potential response of GPP to elevated CO_2 tends to increase along gradients of decreasing precipitation.

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 represented by f(NA) in Eq. 12, is determined by the status of nitrogen supply which is the sum of nitrogen uptake (NUPTAKE) plus nitrogen

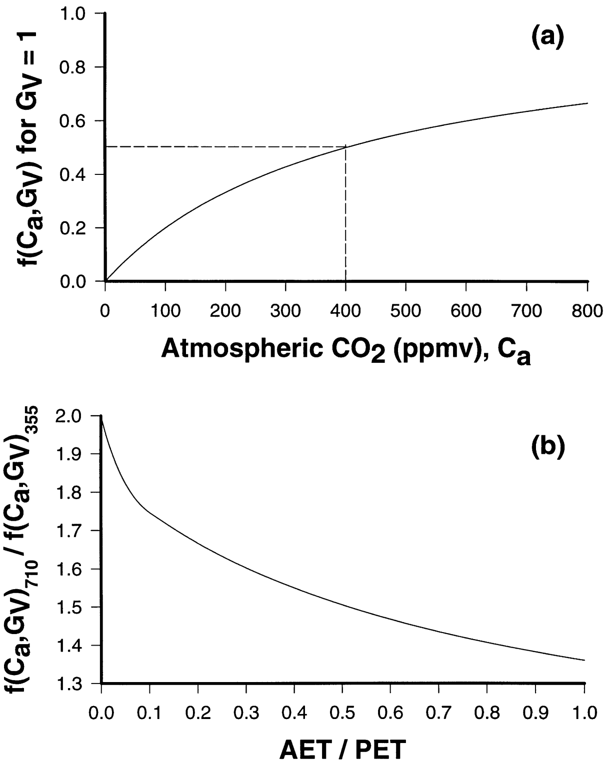

Fig. 6 **a** The hyperbolic scalar function in TEM, f(C_a, G_V), for the effect of atmospheric CO_2 (C_a) and relative canopy conductance (G_V) on gross primary production at G_V equal to 1 vs. atmospheric CO_2 (ppmv). **b** The ratio of the doubled (elevated) scalar function, f(C_a, G_V)$_E$, to the ambient scalar function, f(C_a, G_V)$_A$, vs. a gradient of moisture availability as represented by actual evaportranspiration (AET) and potential evapotranspiration (PET)

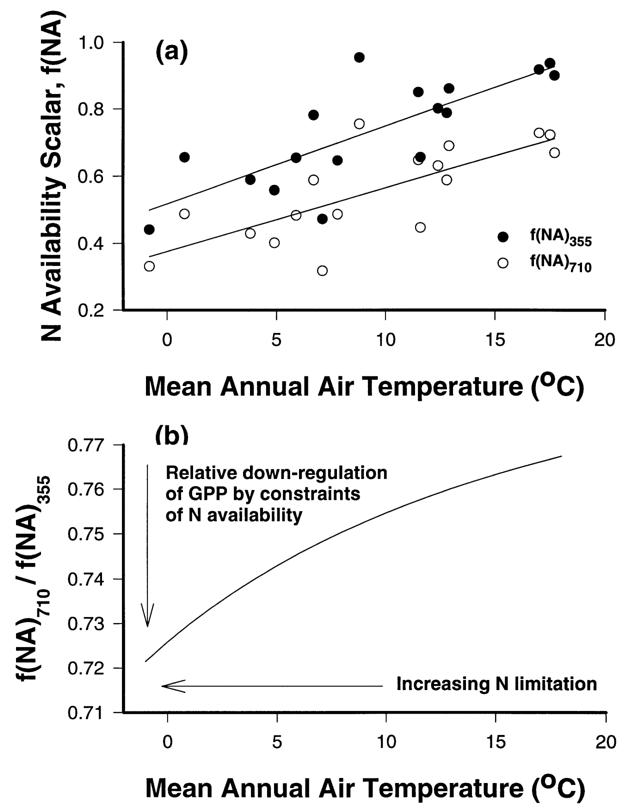

Fig. 7 **a** For each biome within the conterminous United States, the annual scalar for the effect of nitrogen availability on gross primary production, f(NA), vs. mean annual temperature of the biome for two levels of atmospheric CO_2 (355 ppmv and 710 ppmv). The dependence of f(NA) at 355 ppmv is represented by *solid symbols* and at 710 ppmv by *open symbols*; *solid lines* represent linear regressions (355 ppmv: $R = 0.789$; $P = 0.0002$; $n = 17$; 710 ppmv: $R = 0.748$, $P < 0.0001$, $n = 17$). **b** The ratio of the regression lines in **a**, which represents the acclimation response of gross primary production to doubled CO_2 along a gradient of biome mean annual air temperature; the pattern represents down-regulation, which occurs when the photosynthetic capacity of plants grown in elevated CO_2 decreases in comparison to plants grown at baseline CO_2

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. The C to N ratio of production, which is represented by the parameter Pcn, is multiplied by the sum of NUPTAKE and NMOBIL to determine the amount of NPP that can be supported from the nitrogen supply. Nitrogen supply constrains production when the calculation of unconstrained GPP, i.e, potential GPP (GPP_p) for f(NA) equal to 1, exceeds the sum of autotrophic respiration (R_A) and NPP that is determined from nitrogen supply. Therefore, the feedback of nitrogen availability on carbon assimilation, f(NA), is the ratio of GPP to GPP_p (see Appendix). The ability of the vegetation to incorporate elevated atmospheric CO_2 into production as formulated by Eq. 13 depends on the degree to which production is limited by nitrogen supply.

In a nitrogen-limited system we can express f(NA) as:

$$\mathrm{f(NA)} = \frac{\mathrm{GPP}}{\mathrm{GPP_p}} = \frac{\mathrm{Pcn\,(NUPTAKE + NMOBIL)} + R_A}{\mathrm{GPP_p}} \tag{14}$$

In Eq. 14, NUPTAKE is a function of monthly temperature and mean monthly volumetric soil moisture; autotrophic respiration (R_A) is a function of temperature (see Appendix). The behavior of Eq. 14 across climatic gradients is difficult to analyze in an *a priori* fashion because simulation is required to determine the effects of climate on the pools in the equation (see Appendix). However, we can evaluate how nitrogen feedback influences nitrogen limitation of NPP in an *a posteriori* fashion to gain insight into the CO_2 response of production along climatic gradients. The degree to which GPP is limited by nitrogen availability in TEM can be determined by running the model with nitrogen feedback in the GPP equation turned off, i.e., f(NA) = 1, to produce an estimate of GPP that is not limited by nitrogen availability (see McGuire et al. 1992, 1993 for application of this technique). The relative limitation of GPP by nitrogen availability, i.e., f(NA), is calculated as GPP/GPP_p where GPP is the estimate of GPP in the nitrogen-limited solution and GPP_p is the estimate of GPP in the unlimited solution. For both contemporary CO_2 and doubled CO_2, nitrogen limitation of GPP decreases [i.e., f(NA) increases] in ecosystems with higher mean annual temperature (Fig. 7a; $R = 0.789$, $P = 0.0002$ for contemporary CO_2; $R = 0.748$, $P < 0.0001$ for doubled CO_2; $n = 17$ ecosystems), but is unrelated to annual precipitation ($R = 0.052$, $P = 0.8437$ for contemporary CO_2; $R = 0.035$, $P = 0.8948$ for doubled CO_2; $n = 17$). Thus, nitrogen limitation of production tends to increase with decreasing temperature. This relationship indicates that nitrogen supply will tend to constrain the response of NPP to elevated CO_2 more at low temperature than at high temperature.

The observed acclimation response of carbon assimilation, which can be described by the ratio $f(NA)_{2\times CO_2}/f(NA)_{1\times CO_2}$ (Fig. 7b), is categorized as down-regulation. Down-regulation occurs when the photosynthetic capacity of plants grown in elevated CO_2 decreases in comparison to plants grown at baseline CO_2, but the rate of photosynthesis for plants grown and measured at elevated CO_2 is not less than the rate for plants grown and measured at baseline CO_2 (Luo et al. 1994). Because nitrogen supply is least limiting at high temperatures, and the response of NPP tends to be greater for conditions of lower moisture availability, the greatest response of NPP to elevated CO_2 tends to occur in hot and dry ecosystems (Figs. 1a, b, 2c, 6b, 7b).

Discussion

Among the VEMAP biogeochemistry models, doubled atmospheric CO_2 causes simulated increases in NPP for the conterminous United States to increase between 5% and 11%. These increases are substantially lower than the 25–50% growth response to doubled CO_2 that has been observed in greenhouse studies that supply plants with sufficient water and nutrients (Kimball 1975; Gates 1985). In this study, we analyzed the climatic sensitivity of the NPP responses simulated by the models to understand how interactions among carbon, water, and nitrogen dynamics constrain the response of NPP to be less than optimal. The comparison among the three biogeochemistry models in this study indicates that the models tend to agree on NPP responses to doubled CO_2 along precipitation gradients, but tend to disagree on the responses along temperature gradients.

Because there is little information on the relative ecosystem-level responses of NPP to elevated CO_2 along climatic gradients, the controls over the response are not well understood. This lack of understanding has led the models in this study to different conceptualizations about how ecosystem processes control the response of NPP to elevated CO_2. In BIOME-BGC, the NPP response to doubled CO_2 is directly affected by increased intercellular CO_2 concentration and efficiency of quantum yield, reduced canopy conductance, and leaf N concentration. The effects of these factors on NPP do not vary with climate. The patterns of NPP responses along the climate gradients are controlled by the change in transpiration associated with reduced leaf conductance to water vapor. This change affects soil water, then leaf area development, and finally NPP. In Century, the response of NPP to doubled CO_2 is directly affected by increased CO_2 concentration, changes in soil moisture associated with reduced transpiration, and increased C:N ratios in plant foliage. The effects of these factors do not influence NPP responses along climatic gradients. The NPP responses along climate gradients are controlled by changes in decomposition rates associated with increased soil moisture that results from reduced evapotranspiration. This change affects N availability for plants, which influences NPP. In TEM, the NPP response to doubled CO_2 is controlled by increased carboxylation which is modified by canopy conductance and the degree to which nitrogen constraints cause down-regulation of photosynthesis. These factors affect the NPP response along the climate gradients. The implementation of different mechanisms among the models has consequences for the spatial pattern of NPP responses estimated by the models, and represents, in part, conceptual uncertainty about controls over NPP responses.

The NPP estimates for contemporary climate and CO_2 have been extensively tested at specific sites for each of the models in this study (McGuire et al. 1992; Melillo et al. 1993; Parton et al. 1994; Running 1994). The models generally agree on NPP estimates for contemporary conditions at continental and biome scales, but disagree on important details of within-biome patterns (VEMAP members 1995; Schimel et al. 1997). The processes controlling the CO_2 response of NPP in the models are a subset of the processes that have been highlighted in CO_2-enhancement experiments; none of the models have attempted to implement all of the mechanisms that might play a role in controlling ecosystem-level responses of NPP to elevated CO_2. The choice of processes reflects, in part, the different paths of historical development by the models. These biases have both strengths and weaknesses.

The BIOME-BGC relies primarily on the hydrological cycle and water availability for controlling carbon uptake (VEMAP members 1995). The patterns of CO_2 response along both temperature and precipitation gradients reflect, in part, transpiration responses along these gradients. The transpiration response influences soil moisture, which has effects on leaf area development. The explicit treatment of transpiration and leaf area responses is a strength of the BIOME-BGC approach. In contrast to the treatment of hydrological effects, BIOME-BGC does not fully implement the effects of nitrogen availability to control assimilation responses to elevated CO_2. For example, changes in leaf nitrogen are prescribed, and nitrogen cycling plays no role in controlling nitrogen allocated to canopy biomass. Therefore, the response of BIOME-BGC along temperature gradients reflects its focus on transpiration rather than on feedbacks from nutrient cycling.

In contrast to BIOME-BGC, both Century and TEM rely heavily on the nitrogen cycle and nitrogen availability for controlling carbon uptake (VEMAP members 1995; Schimel et al. 1997). Although feedbacks of the nitrogen cycle are important in both Century and TEM, the models differ in how temperature and moisture availability interact to influence nitrogen availability (VEMAP members 1995). In Century, soil water status and C:N ratios in organic matter influence decomposition to affect nitrogen availability to plants. The CO_2-induced changes in soil moisture and C:N ratios of litterfall influence nitrogen availability to affect NPP.

In TEM, the model assumes that leaf area responds so that total canopy conductance and actual evapotranspiration do not change in response to elevated CO_2. The relative response of GPP is potentially greater for lower canopy conductance. Thus, the response of GPP to elevated CO_2 is potentially highest in dry environments. The ability of the vegetation to incorporate elevated atmospheric CO_2 into production according to these hydrological and physiological considerations depends on the degree to which production is limited by nitrogen supply. The feedback between carbon and nitrogen uptake is designed to maintain both the carbon to nitrogen ratios of production and overall vegetative biomass at target ratios that are specific to particular vegetation types. These constraints of carbon-nitrogen status of the vegetation determine the degree to which GPP is down-regulated in response to elevated CO_2. Because nitrogen availability limits production more at low temperature than at high temperature, the response of NPP to elevated CO_2 tends to be lowest in cold mesic environments and to be highest in hot xeric environments. Like Century, TEM explicitly considers interactions between carbon and nitrogen dynamics. Although TEM implicitly considers the interactions between canopy conductance, leaf area, and soil moisture, its approach could be improved by explicitly representing the linkages among these variables. Additionally, the parameters representing the C to N ratios of production were not altered in the simulations. Thus, the effects of lower nitrogen requirement on the ability of vegetation to incorporate elevated CO_2 into production and the effects of higher C to N ratios in reducing decomposition rates were not represented. These effects have been evaluated in an analysis of TEM at the global scale (McGuire et al. 1997). In that analysis, the response of NPP in simulations that considered the combined effects of lower nitrogen requirements and reduced decomposition rates did not differ from the response in simulations that did not include these effects.

The implementation of the mechanisms by the VEMAP biogeochemistry models results from the range of empirical findings observed in various field and laboratory studies (see reviews in Kimball 1975; Kimball and Idso 1983; Eamus and Jarvis 1989; Poorter 1993; Ceulemans and Mousseau 1994; Idso and Idso 1994; McGuire et al. 1995a; Wullschleger et al. 1995). However, these empirical studies do not span the range of environmental and ecosystem conditions that were being simulated in this study. For example, the recent observations on carbon allocation under elevated CO_2 levels (Drake 1992; Owensby et al. 1993) suggest that an increase in carbon allocated to fine-root production is warranted. However, because a general and proven theory for a resource-based approach to allocation does not yet exist (see Running and Hunt 1993), models are forced to adopt a more conservative approach using fixed partitioning coefficients to allocate carbon among plant tissues. Because our experimental understanding is poor, we are unable to validate or verify the responses of the models in this comparison.

In this study, we are able to identify major uncertainties that need to be addressed in future experimental and modeling studies. We have identified four major research priorities from the comparison in this study. (1) What role does the hydrological cycle play in controlling the CO_2 responses of leaf area and soil moisture along temperature and moisture gradients? (2) What role does the nitrogen cycle play in the CO_2 responses of leaf area, and leaf nitrogen content along temperature and moisture gradients? (3) What is the relative role of changes in nitrogen requirements, allocation, tissue C to N ratios, and rates of decomposition in CO_2 responses of NPP along temperature and moisture gradients? (4) What are the relative contributions and importance of interactions between the hydrological and nutrient cycles in controlling NPP responses to elevated CO_2? These are key areas of divergence in conceptual and quantitative models arising from different formulations of the effects of CO_2 on water and nutrient use, allocation, and on long-term coupling of carbon and nitrogen storage (see VEMAP members 1995). Our analysis indicates that additional research is required to understand how interactions between the carbon, nitrogen, and water cycles influence the response of NPP to elevated atmospheric CO_2 in terrestrial ecosystems. In future studies of CO_2 responses, it is important to simultaneously measure carbon, water, and nutrient fluxes and pools in terrestrial ecosystems. Fluxes to be measured should include photosynthesis, decomposition, N uptake, N mineralization, N losses, and evapotranspiration. Pools to be measured should include soil moisture, and the C and N pools in fine roots, wood, leaves, and soil. Measurement of these fluxes and pools is important for understanding the interactions among processes that control CO_2 responses of ecosystems. Progress in understanding these interactions is crucial in reducing the uncertainties about terrestrial responses to elevated atmospheric CO_2.

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Appendix

Analysis of climatic sensitivity of BIOME-BGC responses to doubled CO_2

Temperature sensitivity of transpiration

Transpiration in BIOME-BGC, which is based on the Penman-Monteith formulation, is expressed as:

$$\mathrm{TS} = \frac{\mathrm{SLOPE\ RAD} + (\mathrm{CP\ PA})\mathrm{VPD}/\mathrm{RA}}{\mathrm{SLOPE} + \mathrm{GAMMA}\,\{1 + 1/(G\,\mathrm{RA})\}}\left(\frac{\mathrm{DAYL}}{\mathrm{LE}\ 1000}\right) \tag{A1}$$

where TS is canopy transpiration ($\mathrm{m}^3\ \mathrm{day}^{-1}$); SLOPE is the derivative of humidity deficit (mbar $°\mathrm{C}^{-1}$) at ambient air temperature (T); RAD is average canopy net radiation ($\mathrm{W\ m}^{-2}$); CP is specific heat of air ($\mathrm{J\ kg}^{-1}\ °\mathrm{C}^{-1}$); PA is density of air ($\mathrm{kg\ m}^{-3}$); VPD is vapor pressure deficit from canopy to air (mbar); RA is canopy aerodynamic resistance, which is fixed at 1.0 $\mathrm{s\ m}^{-1}$ for trees and shrubs, and 0.01 $\mathrm{s\ m}^{-1}$ for all grasses; G is leaf conductance ($\mathrm{s\ m}^{-1}$); GAMMA is the psychometric constant (mbar $°\mathrm{C}^{-1}$); LE is latent heat of vaporization of water ($\mathrm{J\ kg}^{-1}$); and DAYL is daylength ($\mathrm{s\ day}^{-1}$). To determine the temperature and moisture sensitivity of transpiration, we simplify Eq. A1 by replacing terms that do not depend on temperature and moisture with constants ($\mathrm{m_x}$). By letting $\mathrm{m_1}$ = RAD, $\mathrm{m_2}$ = CP PA/RA, $\mathrm{m_3}$ = GAMMA, $\mathrm{m_4}$ = GAMMA/RA, and $\mathrm{m_5}$ = DAYL/(LE 1000), Eq. Al is simplified as:

$$\mathrm{TS} = \frac{\mathrm{m_1\ SLOPE + m_2\ VPD}}{\mathrm{SLOPE} + \mathrm{m_3} + \mathrm{m_4}/G}\mathrm{m_5} \tag{A2}$$

With a prescribed 20% reduction in canopy conductance (G), the change in transpiration is expressed as:

$$\begin{aligned}\Delta\mathrm{TS} = \mathrm{TS}_{2\times\mathrm{CO_2}} - \mathrm{TS}_{1\times\mathrm{CO_2}} &= \frac{\mathrm{m_1\ SLOPE\ +\ m_2\ VPD}}{\mathrm{SLOPE\ +\ m_3} + \mathrm{m_4}/G_{2\times\mathrm{CO_2}}}\mathrm{m_5} \\ &\quad - \frac{\mathrm{m_1\ SLOPE\ +\ m_2\ VPD}}{\mathrm{SLOPE\ +\ m_3} + \mathrm{m_4}/G_{1\times\mathrm{CO_2}}}\mathrm{m_5} \\ &= \frac{\mathrm{m_1\ SLOPE\ +\ m_2\ VPD}}{\mathrm{SLOPE\ +\ m_3} + \mathrm{m_4}/(0.8 \times G_{1\times\mathrm{CO_2}})}\mathrm{m_5} \\ &\quad - \frac{\mathrm{m_1\ SLOPE\ +\ m_2\ VPD}}{\mathrm{SLOPE\ +\ m_3} + \mathrm{m_4}/G_{1\times\mathrm{CO_2}}}\mathrm{m_5} \\ &= -0.25\frac{\mathrm{m_4\ m_5(m_1\ SLOPE + m_2\ VPD)}/G_{1\times\mathrm{CO_2}}}{(\mathrm{SLOPE} + \mathrm{m_3} + 1.25\,\mathrm{m_4}/G_{1\times\mathrm{CO_2}})(\mathrm{SLOPE} + \mathrm{m_3} + \mathrm{m_4}/G_{1\times\mathrm{CO_2}})}\end{aligned} \tag{A3}$$

In Eq. A3, both vapor pressure deficit (VPD) and SLOPE depend on temperature:

$$\mathrm{VPD} = 6.1078\mathrm{e}^{17.27T/(237.3+T)} \tag{A4}$$

and

$$\mathrm{SLOPE} = \frac{\mathrm{d(VPD)}}{\mathrm{d}T} = 6.1078\mathrm{e}^{17.27T/(237.3+T)}\,\frac{4098 + 34.54T}{(237.3 + T)^2} \tag{A5}$$

where T is temperature. By substituting these relationships into Eq. A3, we are able to calculate the temperature sensitivity of the relative reduction of transpiration associated with doubled atmospheric CO_2 (see Fig. 3a).

Moisture sensitivity of transpiration

To determine the moisture sensitivity of transpiration, we simplify Eq. A3 by letting $\mathrm{m_6}$ = $\mathrm{m_4\ m_5}$ ($\mathrm{m_1}$ SLOPE + $\mathrm{m_2}$ VPD), and $\mathrm{m_7}$ = SLOPE + $\mathrm{m_3}$, so that the reduction in transpiration only depends on variables that are sensitive to moisture (G, m6, and m7):

$$\Delta\mathrm{TS} = -0.25\ \frac{\mathrm{m_6}}{\dfrac{(\mathrm{m_7}\ G_{1\times\mathrm{CO_2}})^2 + 1.25\,(\mathrm{m_4})^2}{G_{1\times\mathrm{CO_2}}} + 2.25\,\mathrm{m_4\ m_7}} \tag{A6}$$

The greatest potential reduction in transpiration (most negative) will occur when the denominator of Eq. A6 is minimized. To determine canopy conductance, G, associated with the greatest reduction in transpiration we define the variable F_G:

$$F_G = \frac{(\mathrm{m_7}\ G_{1\times\mathrm{CO_2}})^2 + 1.25\,(\mathrm{m_4})^2}{G_{1\times\mathrm{CO_2}}} \tag{A7}$$

and differentiate as follows:

$$\frac{\mathrm{d}F_G}{\mathrm{d}G} = \left[\frac{(\mathrm{m_7}\ G)^2 + 1.25\,(\mathrm{m_4})^2}{G}\right] = 0 \tag{A8}$$

and determine that F_G is maximized when

$$G = \sqrt{\frac{1.25(\mathrm{m_4})^2}{2\mathrm{m_7} - \mathrm{m_7}^2}} = \sqrt{\frac{1.25(\mathrm{m_3}/5)^2}{2\mathrm{m_7} - \mathrm{m_7}^2}} \tag{A9}$$

The value of G that minimizes F_G at 10°C is 0.000174 $\mathrm{m\ s}^{-1}$, which is determined by setting $\mathrm{m_3}$, which represents GAMMA, equal to 0.652 (see Monteith 1973), and calculating $\mathrm{m_7}$, which is SLOPE + $\mathrm{m_3}$, as 1.543. Because canopy conductance is related to soil moisture (SWC) through several equations, we can determine the soil moisture associated with the greatest potential reduction in transpiration.

In BIOME-BGC, canopy conductance is expressed as:

$$G = G_{\max} - \mathrm{DG_w}(\mathrm{LWP} - \mathrm{LWP_{min}}) \tag{A10}$$

where G is canopy conductance ($\mathrm{m\ s}^{-1}$); $G_{\max}$ is maximum canopy conductance ($\mathrm{m\ s}^{-1}$); DGw is the slope of G vs. LWP ($\mathrm{m\ s}^{-1}\ {-\mathrm{MPa}}^{-1}$) (=0.00139); LWP is the daily maximum leaf water potential (−MPa); and $\mathrm{LWP_{min}}$ is the minimum leaf water potential inducing stomatal closure, defined here as the spring minimum LWP (−Mpa) (=0.5). Leaf water potential (LWP) in Eq. A10 is calculated by the equation:

$$\mathrm{LWP} = 0.2\ \frac{1}{\mathrm{SWC}/\mathrm{MAXH_2O}} \tag{A11}$$

where SWC is soil water content; and $\mathrm{MAXH_2O}$ is the maximum water-holding capacity (m^3) (=2350). With Eqs. A10 and A11 we determine that the soil moisture that minimizes canopy conductance corresponds to SWC equal to 30.8 mm. Thus, the potential relative reduction in transpiration (−ΔTR) to doubled CO_2 will monotonically increase with soil moisture when SWC is less than 30.8 mm, and will monotonically decrease with soil moisture when SWC is greater than 30.8 mm (see Fig. 3b). In BIOME-BGC, potential reductions in transpiration translate into increases in leaf area.

Leaf area response to potential reductions in transpiration

In BIOME-BGC, decreases in transpiration affect allocation to leaf tissue through the following relationship:

$$\mathrm{LAI} = \mathrm{C_{LWP}\ SLA} = \mathrm{C_{LC}}\ \frac{\mathrm{LWP_{max}}}{\mathrm{LWP_L}}\ \mathrm{SLA} \tag{A12}$$

where $\mathrm{C_{LWP}}$ is carbon available for leaf growth; SLA is specific leaf area ($\mathrm{m^2\ kg^{-1}\ C}$); $\mathrm{C_{LC}}$ is the upper limit on the carbon available for leaf growth; $\mathrm{LWP_{max}}$ is maximum leaf water potential; and $\mathrm{LWP_L}$ is the highest simulated predawn leaf water potential. Based on Eqs. A11 and A12, we determine that the relationship between leaf water potential and soil moisture is:

$$\begin{aligned}\frac{\mathrm{LAI}_{2\times\mathrm{CO_2}}}{\mathrm{LAI}_{1\times\mathrm{CO_2}}} &= \frac{\mathrm{C_{LC}}\,\dfrac{\mathrm{LWP_{max}}}{\mathrm{LWP}_{\mathrm{L}_{2\times\mathrm{CO_2}}}}\ \mathrm{SLA}}{\mathrm{C_{LC}}\,\dfrac{\mathrm{LWP_{max}}}{\mathrm{LWP}_{\mathrm{L}_{1\times\mathrm{CO_2}}}}\ \mathrm{SLA}} = \frac{\mathrm{LWP}_{\mathrm{L}_{1\times\mathrm{CO_2}}}}{\mathrm{LWP}_{\mathrm{L}_{2\times\mathrm{CO2}}}} \\ &= \frac{\mathrm{SWC}_{2\times\mathrm{CO_2}}}{\mathrm{SWC}_{1\times\mathrm{CO_2}}} = \frac{\mathrm{SWC}_{1\times\mathrm{CO_2}} + \Delta\mathrm{SWC}}{\mathrm{SWC}_{1\times\mathrm{CO_2}}} = 1 + \frac{\Delta\mathrm{SWC}}{\mathrm{SWC}}\end{aligned} \tag{A13}$$

where $\mathrm{LAI}_{2\times\mathrm{CO}_2}$ is the leaf area index for doubled atmospheric CO_2, $\mathrm{LAI}_{1\times\mathrm{CO}_2}$ is leaf area index for contemporary atmospheric CO_2, SWC is the soil moisture for contemporary atmospheric CO_2, and ΔSWC is the potential change in soil moisture caused by the potential reduction in transpiration. Thus, in BIOME-BGC, the greatest relative increase in leaf area is associated with the greatest potential relative increase in soil moisture, which tends to be associated with the greatest potential relative decrease in transpiration. Because, increases in leaf area enhance gross primary production (GPP) in BIOME-BGC, increases in leaf area will also enhance NPP.

Canopy conductance and nitrogen feedback in TEM

Calculation of relative canopy conductance

In TEM, relative canopy conductance, G_V, can be expressed as:

$$\begin{cases} G_V = -10\left(\frac{\mathrm{AET}}{\mathrm{PET}}\right)^2 + 2.9\frac{\mathrm{AET}}{\mathrm{PET}} & \text{when } \frac{\mathrm{AET}}{\mathrm{PET}} \le 0.1 \\ G_V = 0.1 + 0.9\frac{\mathrm{AET}}{\mathrm{PET}} & \text{when } \frac{\mathrm{AET}}{\mathrm{PET}} > 0.1 \end{cases} \tag{A14}$$

where AET is actual evapotranspiration and PET is potential evapotranspiration. G_V increases monotonically with the ratio of AET/PET.

Calculation of f(NA), the nitrogen feedback scalar

In TEM, the feedback of nitrogen availability on carbon assimilation, f(NA), is dynamically determined by comparing the calculation of GPP based on nitrogen supply and the calculation of potential GPP for no constraints of nitrogen supply. Potential GPP, $\mathrm{GPP_p}$, is calculated as:

$$\mathrm{GPP_p} = C_{\max}\mathrm{f(PAR)\ f(LEAF)\ f}(T)\mathrm{f}(\mathrm{C_a}, G_V) \tag{A15}$$

where $C_{\max}$ is the maximum rate of C assimilation, PAR is the photosynthetically active radiation, LEAF is leaf area relative to the maximum annual leaf area, T is the monthly air temperature, C_a is the atmospheric concentration of carbon dioxide, and G_V is relative canopy conductance. Monthly GPP, NPP, and f(NA) are calculated in TEM as:

$$\begin{cases} \mathrm{NPP} & = \mathrm{Pcn(NUPTAKE + NMOBIL)} \\ \mathrm{GPP} & = \mathrm{Pcn(NUPTAKE + NMOBIL)} + R_A \\ \mathrm{f(NA)} & = \mathrm{GPP/GPP_p} \\ \text{when} & \mathrm{Pcn(NUPTAKE + NMOBIL)} + R_A < \mathrm{GPP_p} \end{cases} \tag{A16}$$

and

$$\begin{cases} \mathrm{NPP} & = \mathrm{GPP_p} - R_A \\ \mathrm{GPP} & = \mathrm{GPP_p} \\ \mathrm{f(NA)} & = 1 \\ \text{when} & \mathrm{Pcn(NUPTAKE + NMOBIL)} + \mathrm{R_A} \ge \mathrm{GPP_p} \end{cases} \tag{A17}$$

where Pcn is the C to N ratio of production, NUPTAKE is nitrogen uptake, NMOBIL is nitrogen mobilized from the vegetation labile nitrogen pool, and R_A is autotrophic respiration. From Eq. A16, f(NA) in a nitrogen-limited system is expressed as:

$$\mathrm{f(NA)} = \frac{\mathrm{GPP}}{\mathrm{GPP_p}} = \frac{\mathrm{Pcn\ (NUPTAKE + NMOBIL)} + R_A}{\mathrm{GPP_p}} \tag{A18}$$

In TEM, NUPTAKE is expressed as:

$$\mathrm{NUPTAKE} = \mathrm{N_{max}\ f(N_{AV}, S_{MV})\ f}(T)\ \mathrm{f(CA)} \tag{A19}$$

where N_{max} is the maximum rate of N uptake by the vegetation, N_{AV} is the mean monthly pool of inorganic nitrogen available in the soil solution, SM_V is mean monthly volumetric soil moisture, T is mean monthly temperature, and CA is carbon availability (see McGuire et al. 1992, 1997). The function f(N_{AV}, SM_V) is described by the hyperbolic (Michaelis-Mention) function:

$$\mathrm{f(N_{AV}, SM_V)} = \frac{(\mathrm{SM_V})^3\ \mathrm{N_{AV}}}{\mathrm{k_{n1}} + (\mathrm{SM_V})^3\ \mathrm{N_{AV}}} \tag{A20}$$

where k_{n1} is the half-saturation constant for nitrogen uptake. The function f(T) in the NUPTAKE equation is an exponential function with a Q_{10} of 2.0. When N supply limits plant growth, f(CA) is equal to 1 because carbon is not a limited factor for N uptake [see McGuire et al. 1992 for more details on f(CA)].

The sum of autotrophic respiration (R_A) is expressed as:

$$R_A = R_m + R_g = K_r\ \mathrm{C_V}\ e^{(\ln \mathrm{Q_{10r}}/10)T} + R_g \tag{A21}$$

where R_m is maintenance respiration, and R_g is growth respiration, K_r is the basal respiration rate of vegetation carbon, C_V is vegetation carbon, Q_{10r} is the Q_{10} of respiration (see McGuire et al. 1992). Because growth respiration is calculated as 20% of the photosynthate that is available for the construction of new tissue, GPP can be calculated as (see Raich et al. 1991):

$$\mathrm{GPP} = 1.25\mathrm{NPP} + R_m \tag{A22}$$

The substitution of Eqs. A19–22 into Eq. A18 yields:

$$\begin{aligned} \mathrm{f(NA)} &= \frac{\mathrm{GPP}}{\mathrm{GPP_p}} = \frac{1.25\mathrm{NPP} + R_m}{\mathrm{GPP}_p} \\ &= \frac{1.25\mathrm{Pcn(NUPTAKE + NMOBIL)} + R_m}{\mathrm{GPP_p}} \\ &= \frac{1.25\mathrm{Pcn}\left(\mathrm{N_{max}}\frac{(\mathrm{SM_V})^3\mathrm{N_{AV}}}{\mathrm{k_{n1}}+(\mathrm{SM_V})^3\mathrm{N_{AV}}}e^{0.693T} + \mathrm{NMOBIL}\right) + K_r\mathrm{C_V}\,e^{(\ln \mathrm{Q_{10r}}/10)T}}{C_{\max}\ \mathrm{f(PAR)\ f(LEAF)\ f}(T)\ \mathrm{f}(\mathrm{C_a}, G_V)} \end{aligned} \tag{A23}$$

Equation A23 indicates that the feedback of nitrogen availability on carbon assimilation is influenced by two nitrogen pools (N_{AV}, NMOBIL), one carbon pool (C_V), soil moisture (SM_V) and air temperature (T).

References

Arnone JA III, Körner C (1995) Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. Oecologia 104: 61–71

Bernston GM, Bazzaz FA (1997) Nitrogen cycling in microcosms of yellow birch exposed to elevated CO_2: simultaneous positive and negative below-ground feedbacks. Global Change Biol 3: 247–258

Canadell JG, Pitelka LF, Ingram JSI (1996) The effects of elevated CO_2 on plant-soil carbon below-ground: a summary and synthesis. Plant Soil 187: 391–400

Cardon ZG (1996) Effects of root exudation and rhizodeposition on ecosystem carbon storage under elevated CO_2. Plant Soil 187: 277–288

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO_2 on wood plants. New Phytol 127: 425–426

Curtis PS (1996) A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant Cell Environ 19: 127–137

Curtis PS, Balduman LM, Drake BG, Whigham DF (1990) The effect of elevated atmospheric CO_2 on belowground processes in C_3 and C_4 estuarine marsh communities. Ecology 71: 2001–2006

Day FP, Weber EP, Hinkle CR, Drake BG (1996) Effects of elevated atmospheric CO_2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. Global Change Biol 2: 143–148

Drake BG (1992) The impact of raising CO_2 on ecosystem production. Water Air Soil Pollut 64: 25–44

Drake BG, Leadley PW, Arp WJ, Nassiry D, Curtis P (1989) An open top chamber for controlling CO_2 concentration and measuring net ecosystem gas exchange. Funct Ecol 3: 363–371

Drake BG, Peresta G, Beugeling E, Matamala R (1996) Long-term elevated CO_2 exposure in a Chesapeake Bay wetland: ecosystem gas exchange, primary production, and tissue nitrogen. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 197–214

Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Adv Ecol Res 19: 1–55

Ellsworth DS, Oren R, Huang C, Phillips N, Hendrey GR (1995) Leaf and canopy responses to elevated CO_2 in a pine forest under free-air CO_2 enrichment. Oecologia 104: 139–146

Farquhar GD, Caemmerer S von, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149: 78–90

Field CB, Chapin FS III, Chiariello NR, Holland EA, Mooney HA (1996) The Jasper ridge CO_2 experiment: design and motivation. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 212–145

Field CB, Lund CP, Chiariello NR, Mortimer BE (1997) CO_2 effects on the water budget of grassland microcosm communities. Global Change Biol 3: 197–206

Franck VM, Hungate BA, Chapin FS III, Field CB (1997) Decomposition of litter produced under elevated CO_2: dependence on plant species and nutrient supply. Biogeochemistry 36: 223–237

Gates DM (1985) Global biospheric response to increasing atmospheric carbon dioxide concentration. In: Strain BR, Cure JD (eds) Direct effects of increasing carbon dioxide on vegetation. Report DOE/ER-0238, US Department of Energy, Washington, DC pp 171–184

Grulke NE, Riechers GH, Oechel WC, Hjelm U, Jaeger C (1990) Carbon balance in tussock tundra under ambient and elevated CO_2. Oecologia 83: 485–484

Hungate BA, Jackson RB, Field CB, Chapin III FS (1996) Field CO_2 enrichment experiments lack statistical power to detect changes in soil carbon. Plant Soil 187: 135–145

Hungate B, Chapin FS III, Zhong H, Field CB (1997) Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. Oecologia 109: 149–153

Hunt ER Jr, Running SW (1992) Simulated dry matter yields for aspen and spruce stands in the North American boreal forest. Can J Remote Sensing 3: 126–133

Idso KE, Idso SB (1994) Plant response to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the last 10 years' research. Agric For Meteorol 69: 153–203

IPCC WG1 (1996) Technical summary. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate change 1995 – the science of climate change: contribution of working group I to the second assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK, pp 9–50

Jackson RB, Sala OE, Field CB, Mooney HA (1994) CO_2 alters water use, carbon gain, and yield for the dominant species in a natural grassland. Oecologia 98: 257–262

Johnson DJ, Henderson PH, Ball JT, Walker RF (1996) Effects of CO_2 and N on growth and N dynamics in Ponderosa pine: results from the first two growing seasons. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 23–40

Kemp PR, Waldecker DG, Owensby CE, Reynolds JF, Virginia RA (1994) Effects of elevated CO_2 and nitrogen fertilization pretreatments on decomposition on tallgrass prairie leaf litter. Plant Soil 165: 115–127

Kimball BA (1975) Carbon dioxide and agriculture yield: an assemblage and analysis of 430 prior observations. Agron J 75: 779–788

Kimball BA, Idso SB (1983) Increasing atmospheric CO_2: effects on crop yield, water use and climate. Agric Water Manager 7: 55–72

Kittel TGF, Rosenbloom NA, Painter TH, Schimel DS, VEMAP modeling participants (1995) The VEMAP integrated database for modeling United States ecosystem/vegetation sensitivity to climate change. J Biogeog 22: 857–862

Kittel TGF, Rosenbloom NA, Painter TH, Schimel DS, Fisher HH, Grimsdell AW, VEMAP participants, Daly C, Hunt ER Jr (1996) The VEMAP phase 1 database: an integrated input dataset for ecosystem and vegetation modeling for the conterminous, United States. CD-ROM. National Center for Atmospheric Research, Boulder, Colo

Koch GW, Mooney HA (eds) (1996) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego

Körner C, Arnone JA III (1992) Responses to elevated carbon dioxide in artificial tropical ecosystems. Science 257: 1672–1675

Körner C, Bazzaz FA (1996) Carbon dioxide, populations, and communities. Academic Press, San Diego

Körner C, Diemer M, Schäppi B, Niklaus P, Arnone J (in press) The response of alpine grassland to four seasons of CO_2 enrichment: a synthesis. Acta Oecol

Leuning R (1990) Modeling stomatal behavior and photosynthesis of *Eucalyptus grandis*. Aust J Plant Physiol 17: 159–175

Luo Y, Field CB, Mooney HA (1994) Predicting response of photosynthesis and root fraction to elevated $[CO_2]a$: interactions among carbon, nitrogen and growth. Plant Cell Environ 17: 1195–1204

McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL, Moore B III, Vorosmarty CJ (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochem Cycles 2: 101–124

McGuire AD, Joyce LA, Kicklighter DW, Melillo JM, Esser G, Vörösmarty CJ (1993) Productivity response of climax temperate forests to elevated temperature and carbon dioxide: a North American comparison between two global models. Climate Change 24: 287–310

McGuire AD, Melillo JM, Joyce LA (1995a) The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon dioxide. Annu Rev Ecol Syst 26: 473–503

McGuire AD, Melillo JM, Kicklighter DW, Joyce LA (1995b) Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates. J Biogeogr 22: 785–796

McGuire AD, Melillo JM, Kicklighter DW, Pan Y, Xiao X, Helfrich J, Moore B III, Vorosmarty CJ, Schloss AL (1997) Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. Global Biogeochem Cycles 11: 173–189

McMurtrie RE, Comins HN, Kirschbaum UFK, Wang YP (1992) Modifying existing forest growth models to take account of effects of elevated CO_2. Aust J Bot 40: 657–677

Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363: 234–240

Melillo JM, Kicklighter DW, McGuire AD, Peterjohn WT, Newkirk KM (1995) Global change and its effects on soil organic carbon stocks. In: Zepp RG, Sonntag C (eds) Role of nonliving organic matter in the earth's carbon cycle. Wiley, New York, pp 175–189

Melillo JM, Prentice IC, Farquhar GD, Schulze E-D, Salo OE (1996) Terrestrial biotic responses to environmental change and feedbacks to climate. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate Change 1995 – the science of climate change: contribution of working group I to the second assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK, pp 445–482

Monteith JL (1973) Principles of environmental physics. Arnold, London

Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF (1991) Predicting ecosystem responses to elevated CO_2 concentrations. Bioscience 2: 96–104

Norby RJ, Gunderson CA, Wullschleger SD, O'Neill EG, McCracken MK (1992) Productivity and compensatory responses of yellow-poplar trees in elevated CO_2. Nature 357: 322–324

Norby RJ, Wullschleger SD, Gunderson CA (1996) Tree responses to elevated CO_2 and implications for forests. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 1–21

Oechel WC, Vourlitis GL (1996) Direct effects of elevated CO_2 on Arctic plant and ecosystem function. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 163–176

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361: 520–523

Owensby CE, Coyne PI, Ham JM, Auen LM, Knapp AK (1993) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. Ecol Appl 3: 644–653

Owensby CE, Ham JM, Knapp A, Rice CW, Coyne PI, Auen LM (1996) Ecosystem-level responses of tallgrass prairie to elevated CO_2. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 147–162

Owensby CE, Ham JM, Knapp AK, Bremer D, Auen LM (1997) Water vapour fluxes and their impact under elevated CO_2 in a C4-tallgrass prairie. Global Change Biol 3: 189–196

Pan Y, McGuire AD, Kicklighter DW, Melillo JM (1996) The importance of climate and soils for estimates of net primary production: a sensitivity analysis with the terrestrial ecosystem model. Global Change Biol 2: 5–23

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci Am J 51: 1173–1179

Parton WJ, Stewart WB, Cole CV (1988) Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5: 109–131

Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut J-C, Seastedt T, Garcia Moya E, Apinan Kamnalrut, Kinyamario JI (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem Cycles 4: 785–809

Parton WJ, Ojima DS, Cole CV, Schimel DS (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: Quantitative modeling of soil forming processes. Soil Science Society of America, Madison, pp 147–167

Parton WJ, Scurlock JMO, Ojima DS, Schimel DS, Hall DO, SCOPEGRAM group members (1995) Impact of climate change on grassland production and soil carbon worldwide. Global Change Biol 1: 13–22

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio 104/105: 77–97

Raich JW, Rastetter EB, Melillo JM, Kicklighter DW, Steudler PA, Peterson BJ, Grace AL, Moore B III, Vorosmarty CJ (1991) Potential net primary productivity in South America: application of a global model. Ecol Appl 4: 399–429

Rastetter EB (1996) Validating models of ecosystem response to global change. Bioscience 46: 190–198

Rice CW, Garcia FO, Hampton CO, Owensby CE (1994) Soil microbial response in tallgrass prairie to elevated CO_2. Plant Soil 165: 67–74

Running SW (1994) Testing forest-BGC ecosystem process simulations across a climatic gradient in Oregon. Ecol Appl 4: 238–247

Running SW, Coughlan JC (1988) A general model of forest ecosystem processes for regional application. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol Model 42: 125–154

Running SW, Gower ST (1991) FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiol 9: 147–160

Running SW, Hunt ER Jr. (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale model. In: Ehleringer JR, Field C (eds) Levels scaling processes between leaf and landscape. Academic Press, San Diego, pp 141–158

Schimel DS, Kittel TGF, Parton WJ (1991) Terrestrial biogeochemical cycles: global interactions with the atmosphere and hydrology. Tellus 43AB: 188–203

Schimel DS, Braswell BH Jr, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend AR (1994) Climate, edaphic, and biotic controls over carbon and turnover of carbon in soils. Global Biogeochem Cycles 8: 279–293

Schimel DS, VEMAP participants, Braswell BH (1997) Continental scale variability in ecosystem processes: models, data and the role of disturbance. Ecol Monogr 67: 251–271

Schortemeyer M, Hartwig UA, Hendrey GR, Sadowsky MJ (in press) Microbial community changes in the rhizospheres of white clover and perennial ryegrass exposed to free air carbon dioxide enrichment (FACE). Soil Biol Biochem

Stocker R, Leadley PW, Körner C (1997). Carbon and water fluxes in a calcareous grassland under elevated CO_2. Funct Ecol 11: 222–230

Strain GR, Cure JD (1994) Direct effects of atmospheric enrichment on plants and ecosystems: an updated bibliographic data base. Oak Ridge National Laboratory/CDIAC-13, Oak Ridge, Tenn

VEMAP members (1995) Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochem Cycles 4: 407–437

Wullschleger SD, Post WM, King AW (1995) On the potential for a CO_2 fertilization effect in forest trees – an assessment of 58 controlled-exposure studies and estimates of biotic growth factor. In: Woodwell GM, Mackenzie FT (eds) Biotic feedbacks in the global climate system. Oxford University Press, New York, pp 85–107

Zak DR, Pregitzer KS, Curtis PS, Teeri JA, Fogel R, Randlett D (1993) Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles. Plant Soil 151: 105–117

Zak DR, Ringelberg DB, Pregitzer KS, Randlett DL, White DC, Curtis PS (1996) Soil microbial communities beneath *Populus grandidentata* grown under elevated atmospheric CO_2. Ecol Appl 6: 257–262