Global climate change and terrestrial net primary production

Jerry M. Melillo*, A. David McGuire*, David W. Kicklighter*, Berrien Moore III†, Charles J. Vorosmarty† & Annette L. Schloss†

* The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA
† Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, New Hampshire 03824, USA

A process-based model was used to estimate global patterns of net primary production and soil nitrogen cycling for contemporary climate conditions and current atmospheric CO_2 concentration. Over half of the global annual net primary production was estimated to occur in the tropics, with most of the production attributable to tropical evergreen forest. The effects of CO_2 doubling and associated climate changes were also explored. The responses in tropical and dry temperate ecosystems were dominated by CO_2, but those in northern and moist temperate ecosystems reflected the effects of temperature on nitrogen availability.

THE atmospheric concentrations of the major long-lived greenhouse gases continue to increase because of human activity[1]. Most climate models predict that the buildup of these gases is likely to lead to surface air temperature rises of 1.5 °C to 4.5 °C and changes in precipitation and cloud patterns over the next century[2]. Climate changes of this magnitude are expected to affect the net primary production (NPP) of the world's land ecosystems[3]. Annual NPP is the net amount of carbon captured by land plants through photosynthesis each year. It is of fundamental importance to humans because the largest portion of our food supply is from productivity of plant life on land, as is wood for construction and fuel. Because climate changes are predicted to vary from place to place[2], estimating the response of NPP will require the use of models that can make geographically referenced predictions. Both regression- and process-based models are available to assess the response of terrestrial NPP with some degree of geographic specificity.

Regression-based models use empirically derived relationships between climate and NPP to make predictions[4]. Although these models can presently be extrapolated for all land ecosystems[5-7], their use for predicting NPP responses is limited because the regressions may not be appropriate for climatic conditions that are novel to terrestrial ecosystems[8]. Unlike regression-based models, process-based models describe how important ecosystem processes such as photosynthesis, respiration, decomposition and nutrient cycling interact to affect NPP. Therefore they have the potential for accurately describing how these processes will interact in future climates[8]. Although process-based models have been used in regional studies to evaluate responses of NPP to climate change in a geographically referenced manner[8-12], none has been applied globally.

Here we report the results of a study in which we use a process-based terrestrial ecosystem model (TEM) to estimate global patterns of NPP for contemporary climate conditions and current atmospheric CO_2. In addition, we use the output from global climate models, known as general circulation models (GCMs), to estimate the potential effects of a CO_2 doubling and associated climate changes on NPP for the world's land ecosystems. We have restricted our analysis to evaluate the equilibrium response of NPP to changes in CO_2 and climate for the vegetation distribution that is appropriate to contemporary climate. We do not consider how the response of vegetation distribution to climate change[13-17] affects NPP.

The terrestrial ecosystem model

The TEM (Fig. 1) is a processed-based ecosystem simulation model that uses spatially referenced information on climate, elevation, soils, vegetation and water availability to make monthly estimates of important carbon and nitrogen fluxes and pool sizes[8,12,18]. Because we use TEM to make equilibrium predictions, its estimates of carbon and nitrogen dynamics apply only to mature, undisturbed vegetation; they do not include the effects of land use.

TABLE 1 Values of vegetation-specific parameters used in the TEM

Vegetation type	P_{cn}*	C_{max}†	K_r†	K_d†	KFALL†	N_{max}†	N_{up}†	NFALL*	T_{min}†	T_{opt}†	T_{max}†	V_{CN}†
Polar desert/alpine tundra	32.50	591.80	0.038900	0.001048	0.012037	1.51000	0.706693	0.006325	−1.0	15.0	36.0	69.23
Wet/moist tundra	30.00	955.50	0.038900	0.000645	0.013333	3.48000	1.533380	0.004410	−1.0	15.0	36.0	50.00
Boreal woodland	45.24	842.00	0.011080	0.000924	0.005871	0.85500	0.205103	0.004692	−1.0	15.0	36.0	91.67
Boreal forest	52.38	676.20	0.002185	0.001396	0.002037	0.70900	0.081884	0.007950	−1.0	15.0	36.0	375.00
Temperate coniferous forest	89.17	1,013.90	0.001316	0.001219	0.001025	0.50000	0.034516	0.004667	−1.0	18.0	39.0	580.00
Desert	30.56	492.00	0.006180	0.000973	0.016975	0.53850	0.142026	0.011540	1.0	31.0	51.0	27.69
Arid shrubland	30.56	492.00	0.006180	0.000973	0.016975	0.53850	0.142026	0.011540	1.0	31.0	51.0	27.69
Short grassland	54.29	779.20	0.017150	0.004323	0.052910	0.45950	0.247182	0.033020	0.0	27.0	45.0	35.80
Tall grassland	69.55	977.35	0.016775	0.001008	0.054487	0.29080	0.138580	0.074720	0.0	27.0	45.0	108.33
Temperate savanna	66.44	1,083.70	0.006975	0.004723	0.018254	0.47020	0.157422	0.029783	−1.0	24.0	46.0	131.25
Temperate deciduous forest	65.00	1,207.90	0.001465	0.002303	0.003483	0.75300	0.073770	0.018090	−1.0	20.0	43.0	426.05
Temperate mixed forest	74.97	1,125.90	0.002255	0.002422	0.003660	0.49862	0.076415	0.015400	−1.0	19.0	41.0	422.29
Temperate broadleaf evergreen forest	90.63	780.75	0.001833	0.002110	0.004028	0.47560	0.073452	0.011905	0.0	25.0	49.0	357.14
Mediterranean shrubland	39.29	614.64	0.003138	0.001841	0.010659	1.10000	0.118475	0.013550	−1.0	25.0	49.0	47.78
Tropical savanna	33.23	1,897.75	0.005481	0.000976	0.005747	0.64650	0.067100	0.007166	1.0	30.0	49.0	41.43
Xeromorphic forest	39.29	614.64	0.003138	0.001841	0.010659	1.10000	0.118475	0.013550	−1.0	25.0	49.0	47.78
Tropical deciduous forest	32.66	1,426.40	0.002657	0.002242	0.005140	3.41400	0.197320	0.010236	0.0	27.0	48.0	66.76
Tropical evergreen forest	43.75	1,034.75	0.001346	0.001250	0.003889	2.83000	0.111000	0.006690	2.0	28.0	48.0	75.00

See Table 2 in ref. 12 for the parameter values of the leaf phenology model, Table 4 in ref. 12 for values of the soil-specific parameters, and Table A2 in ref. 18 for values of the constant parameters k_i, k_{n1} and k_{n2}.

* See ref. 12 for parameter definition.

† See ref. 18 for parameter definition.

For each monthly time step in a model run, NPP is calculated as the difference between gross primary productivity (GPP) and plant respiration (R_A). The calculation of R_A considers both maintenance respiration[8,12] and construction respiration[18]. The flux GPP considers the effects of several factors and is calculated at each time step as follows:

$$\mathrm{GPP} = C_{max} f(\mathrm{PAR}) f(\mathrm{LEAF}) f(T) f(\mathrm{CO_2}, \mathrm{H_2O}) f(\mathrm{NA})$$

where C_{max} is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF is leaf area relative to maximum annual leaf area, T is temperature, CO_2 is atmospheric carbon dioxide, H_2O is water availability, and NA is nitrogen availability. All of the functions in the GPP equation, as well as other mathematical expressions in the model, are well documented in previous work[8,12,18]. Here we review the descriptions of $f(CO_2, H_2O)$ and $f(NA)$ because of their importance in affecting the capacity of the vegetation to incorporate elevated CO_2 into production.

The function $f(CO_2, H_2O)$ is described by the hyperbolic relationship[8,18]:

$$f(\mathrm{CO_2}, \mathrm{H_2O}) = C_i/(k_c + C_i)$$

where C_i is the concentration of CO_2 within leaves of the canopy and k_c is the half-saturation constant for CO_2 uptake by plants. The variable C_i is the product of ambient CO_2 and relative canopy conductance to CO_2, a variable which increases from 0 to 1 with increasing water availability[12,18]. The parameter k_c has been chosen to increase $f(CO_2, H_2O)$ by 37% for a doubling of atmospheric CO_2 from 340 parts per million by volume (p.p.m.v.) to 680 p.p.m.v. with canopy conductance equal to 1 (refs 8, 12). Among studies that have provided adequate water and nutrients to experimental plants, the range in the response of plant growth to doubled CO_2 is between 24% and 50% (refs. 19, 20).

The function $f(NA)$ models the limiting effects of plant nitrogen status on GPP[8,12]. It constrains C uptake when N supply, defined as the combination of N uptake and vegetation labile N, limits production. Information on the C to N ratio of production (P_{cn}), a quantity commonly measured in ecosystem studies, is used to determine when N supply limits production. This implementation assumes that nitrogen use efficiency, defined as the ratio of NPP to N in new production, is conservative within a vegetation type.

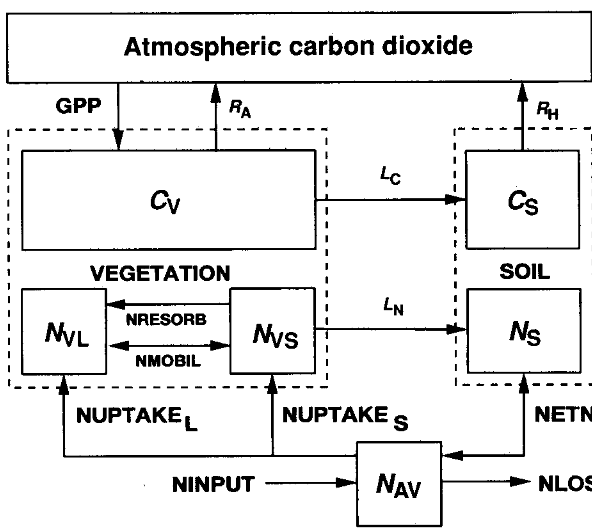

FIG. 1 The terrestrial ecosystem model (TEM). Carbon enters the vegetation pool (C_V) as gross primary productivity (GPP) and transfers to the atmosphere as plant respiration (R_A) or to the soil pool (C_S) as litter production (L_C); it leaves the soil as heterotrophic respiration (R_H). Nitrogen inputs from outside the ecosystem (NINPUT) enter the inorganic N pool (N_{AV}); losses leave this pool as the flux NLOST. Nitrogen in the vegetation occurs either in the structural pool (N_{VS}) or the labile pool (N_{VL}). Structural N in vegetation is constructed from N that is derived from either the labile pool as the flux NMOBIL or from soil inorganic N pool as the flux NUPTAKE$_S$. The labile pool is replenished from N that is resorbed from senescing tissue (NRESORB), N that is allocated for storage (NMOBIL), or N in uptake that does not enter directly into tissue construction (NUPTAKE$_L$). Nitrogen is transferred from vegetation to the soil organic pool (N_S) as the flux L_N. Net N mineralization (NETNMIN) accounts for N exchanged between the organic and inorganic N pools of the soil.

TABLE 2 Estimates by the TEM of annual NPP and nitrogen uptake for potential vegetation in the terrestrial biosphere at an atmospheric concentration of 355 p.p.m.v. CO_2

Vegetation type	Area (10^6 km^2)	Cells	Total NPP (10^{15} g C yr^{-1})	Mean NPP	Max NPP (g C m^{-2} yr^{-1})	Min NPP	Total N uptake (10^{12} g N yr^{-1})	Mean N Uptake (g N m^{-2} yr^{-1})
Polar desert/alpine tundra	5.0	3,147	0.4	87	216	0	3	0.7
Wet/moist tundra	4.7	3,788	0.6	120	423	34	4	0.8
Boreal woodland	6.3	4,414	1.1	173	420	89	9	1.5
Boreal forest	12.2	7,406	2.9	238	434	124	31	2.5
Temperate coniferous forest	2.4	1,081	1.1	465	704	208	9	3.7
Desert	11.5	4,145	0.6	53	370	0	15	1.3
Arid shrubland	14.5	5,708	1.9	129	454	6	46	3.2
Short grassland	4.7	2,050	1.0	214	438	72	17	3.7
Tall grassland	3.6	1,557	1.2	335	756	136	16	4.4
Temperate savanna	6.8	2,886	2.3	342	785	68	29	4.3
Temperate mixed forest	5.1	2,250	3.4	669	1,066	231	37	7.3
Temperate deciduous forest	3.5	1,614	2.2	620	978	81	27	7.6
Temperate broadleaf evergreen forest	3.2	1,205	2.4	741	1,001	322	20	6.2
Mediterranean shrubland	1.4	554	0.5	343	634	32	12	8.7
Tropical savanna	13.7	4,624	5.4	393	786	88	162	11.8
Xeromorphic forest	6.8	2,357	3.1	461	992	0	79	11.7
Tropical deciduous forest	4.6	1,577	4.0	871	1,398	323	121	26.2
Tropical evergreen forest	17.4	5,727	19.1	1,098	1,422	407	436	25.1
Total	127.3	5,6090	53.2	418	1,422	0	1,073	8.4

Ecosystem-based estimates may not sum to totals because of the effects of rounding in reporting those estimates.

The data sets used to drive TEM are gridded at a resolution of 0.5° latitude by 0.5° longitude. The sources for the global data sets on climate (air temperature, precipitation and cloudiness), elevation and soil texture are described elsewhere[18]; the climate data represent long-term averages. The data set of global potential vegetation (Fig. 2) was constructed from a number of sources[21-31]. Hydrological inputs for TEM were determined with a water balance model[32] that uses the climate, elevation, soils and vegetation data.

The application of TEM to a grid cell requires the use of monthly climatic and hydrological data and the soil- and vegetation-specific parameters appropriate to the grid cell. Although many of the vegetation-specific parameters in the model (Table 1) are defined from published information[12,18], some are determined by calibrating the model to the fluxes and pool sizes of an intensively studied field site. Most of the data used to calibrate the model for the 18 vegetation types considered in this study are documented elsewhere[12]. We do not make estimates for grid cells defined as ice, open water, or wetland ecosystems, so that our global extrapolation of TEM requires application of the model to 56,090 grid cells in the terrestrial biosphere. Because wetlands are represented by only 1,466 grid cells, we do not expect their exclusion to affect global estimates of terrestrial NPP substantially.

Global extrapolation for contemporary climate

To estimate carbon and nitrogen dynamics of potential vegetation for 'contemporary' conditions, we applied TEM globally at 355 p.p.m.v. CO_2 using the long-term climate data. Under these conditions, TEM estimates the global annual NPP for potential vegetation to be 53.2 Pg C (10^{15} g C), or 418 g C m^{-2} yr^{-1} (Table 2). Our process-based estimate is similar to many of the estimates that have appeared in the literature[5-7,33-42] (mean: 53.1 Pg C; $N = 13$; range: 40.5 Pg C to 78.0 Pg C; s.d. 9.3 Pg C). Most of the estimates have been calculated by multiplying the mean NPP for an ecosystem, as determined from a literature survey of field studies, by the area of the ecosystem, and then summing across ecosystems[33-41]. A few of the estimates have been determined by regression approaches involving climate variables[5-7] and some consider the effects of land use[6-7,42].

Over half of the global annual NPP occurs in the tropics between the latitudes of 22.5° S and 22.5° N (29.6 Pg C yr^{-1}; Fig. 2). Most of this productivity is attributable to tropical evergreen forest which accounts for 35.9% of the net exchange of CO_2 between terrestrial vegetation and the atmosphere, although it covers only 13.7% of the terrestrial land surface (Table 2). The least productive vegetation types include polar desert, tundra, and desert, which collectively account for 3.0% of terrestrial NPP and cover 16.7% of the terrestrial land area (Table 2). Mean NPP estimates for vegetation types range from 53 g C m^{-2} yr^{-1} for desert to 1,098 g C m^{-2} yr^{-1} for tropical evergreen forest (Table 2). Estimates for individual grid cells range from 0 g C m^{-2} yr^{-1} to 1,422 g C m^{-2} yr^{-1} (Table 2). The variability of NPP estimates by TEM, which reflects spatial heterogeneity in climate and soils, has been evaluated in previous applications of the model[12,18]. The NPP predictions of this study generally compare well with the field measurements used to construct several regression-based global models of NPP[5] (Fig. 3).

Annual nitrogen uptake by global potential vegetation under conditions of contemporary climate and CO_2 is estimated to be 1,073 Tg N (10^{12} g N), or 8.4 g N m^{-2} yr^{-1} (Table 2). Assuming a global nitrogen-use efficiency (NPP/nitrogen uptake) of 50, others have estimated the annual nitrogen cycling in the terrestrial biosphere to be 1,200 Tg N (ref. 43) and 1,400 Tg N (ref. 44). The global nitrogen-use efficiency in this study is also estimated to be 50 (53.2 Pg C yr^{-1}/1,073 Tg N yr^{-1}). Mean estimates of nitrogen uptake for ecosystems range from 0.7 g N m^{-2} yr^{-1} for polar desert to 26.2 g N m^{-2} yr^{-1} in tropical deciduous forest (Table 2). The accuracy of nitrogen cycling estimates by TEM has been evaluated for several ecosystems in a previous application of the model[12].

Future climate scenarios for use with TEM

We obtained the output of four GCMs from the National Center for Atmospheric Research[45]. The simulations estimate equilibrium climates that correspond to a doubling of the atmospheric

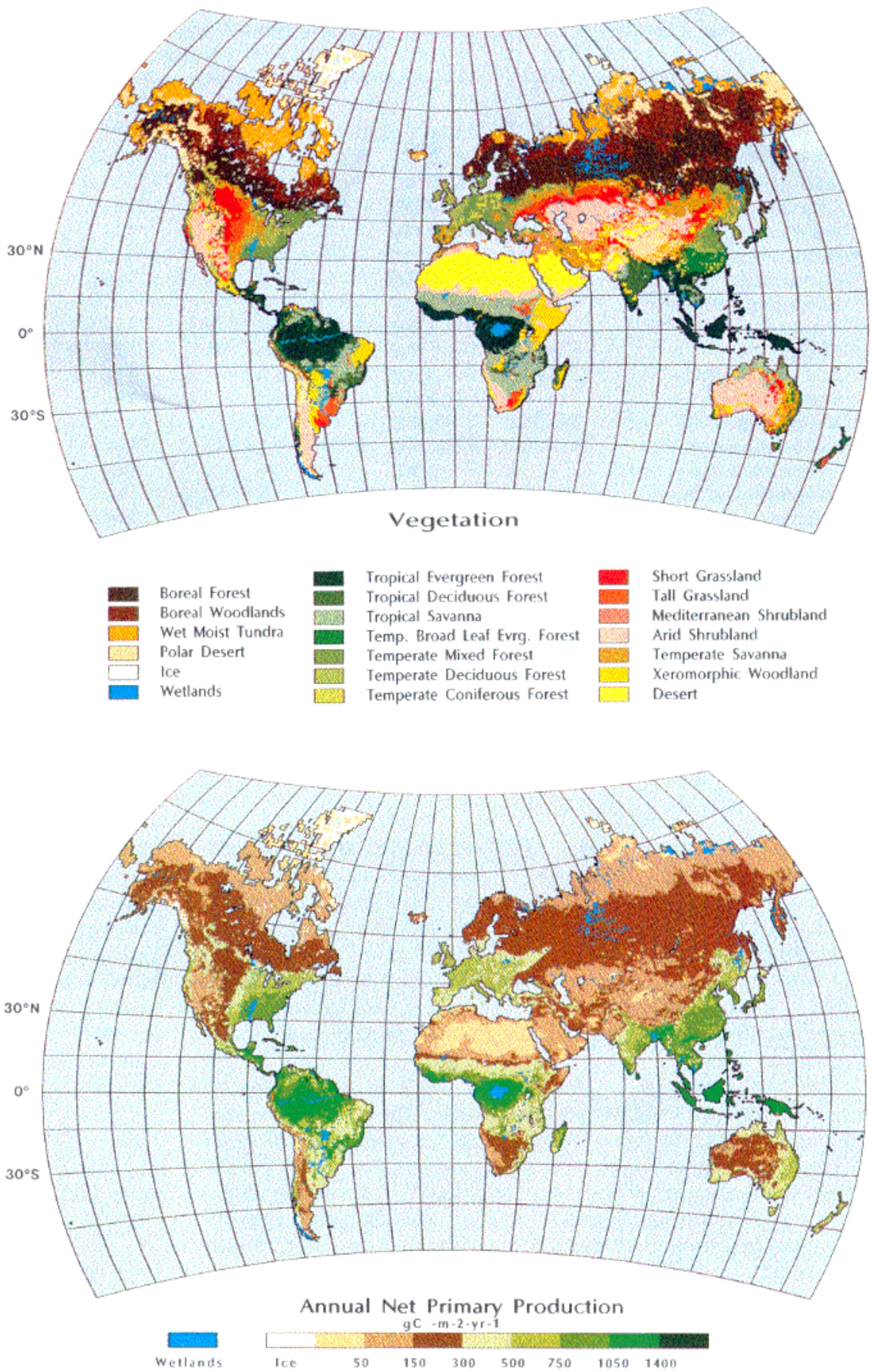

FIG. 2 Potential natural vegetation (top) used by the TEM to estimate annual NPP (bottom) for the global terrestrial biosphere.

CO_2 concentration and include: the Goddard Institute of Space Studies GCM (GISS); the Oregon State University GCM (OSU); and two GCM simulations from the Geophysical Fluid Dynamics Laboratory (GFDL 1 and GFDL Q). Among the GCMs, mean global temperature increases between 2.8 °C and 4.2 °C, global precipitation increases between 7.8% and 11.0%, and global cloudiness decreases between 0.4% and 3.4%.

Because we were interested in the implications of climate change for NPP, we generated 'GCM climates' for TEM by using the output variables of surface air temperature, precipitation, and total cloud cover for the current and $2\times CO_2$ simulations of each GCM to modify the contemporary climate data for TEM. For the heuristic purpose of examining implications at the spatial scale of TEM predictions, we organized each of the output variables of each GCM simulation at the $0.5°\times 0.5°$ resolution with a spherical interpolation procedure[46]. Next, similar to the method used in a study of the potential effects of climate change on US agriculture[47], we calculated for each grid cell the ratio of the monthly output of the $2\times CO_2$ simulation to that of the $1\times CO_2$ simulation for each of the three output variables; temperature was converted to Kelvin before calculating monthly temperature ratios. We then multiplied each ratio by the corresponding variable in our data for contemporary climate to determine the input data for TEM that represent the $2\times CO_2$ climate for each GCM.

To help separate the effects of changes in CO_2 concentration from those of the GCM climates on estimates of NPP, we did a factorial experiment with TEM involving two levels of CO_2 (312.5 p.p.m.v. and 625.0 p.p.m.v.) and five climate scenarios (contemporary and the four GCM climates). We chose the CO_2 level of 312.5 p.p.m.v. because it was the average baseline concentration of the four GCMs (range: 300–326 p.p.m.v.).

NPP responses to doubled CO_2

For doubled CO_2 with no climate change, TEM predicts a global NPP increase of 16.3% (Table 3). The responses differ widely

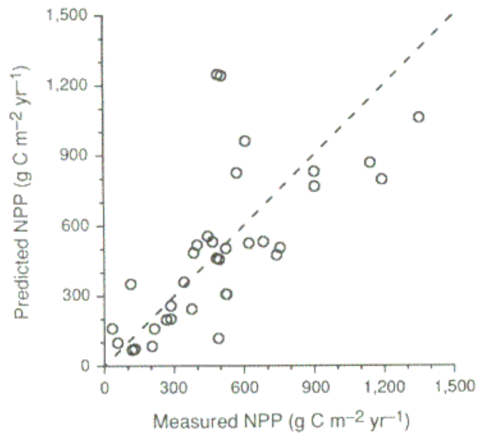

FIG. 3 Comparison between the annual NPP predictions of the TEM and the NPP field measurements that were used to construct several regression-based global models of NPP[5] ($r=0.69$, $N=35$, $P<0.001$). The dashed line indicates equality between predicted and measured NPP.

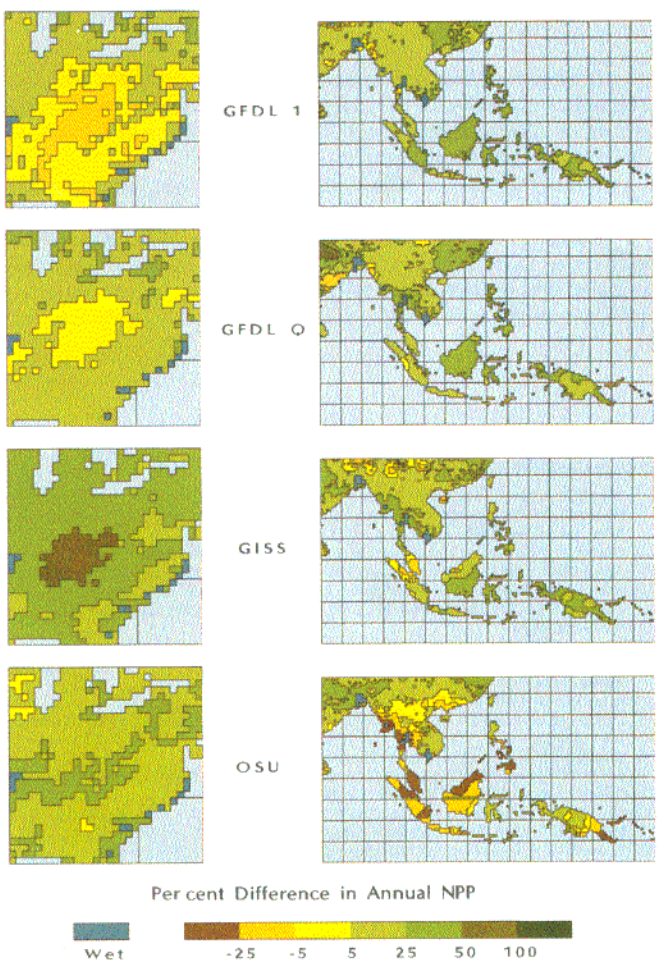

FIG. 4 Per cent difference in annual NPP between contemporary climate at 312.5 p.p.m.v. CO_2 and the various GCM climates at 625.0 p.p.m.v. CO_2 as predicted by the TEM for eastern North America (left) and southeast Asia (right). Estimates were not made for open water (light blue) or wetland ecosystems (bright blue).

among vegetation types and range from no increases for some northern ecosystems to increases of 50.0% for deserts. In general, responses for northern and temperate ecosystems are less than 10%. Responses for many dry ecosystems, such as deserts, arid shrublands, and xeromorphic forests, are over 20%. Tropical evergreen forests, which experience an increase of 22.2% or 4.0 Pg C per year, account for about half of the global increase.

In many northern and temperate ecosystems, NPP is known to be limited by the availability of inorganic nitrogen in the soil[48]. Because of nitrogen limitation, TEM predicts that these ecosystems have low capacity to incorporate elevated CO_2 into production[7]. In nutrient-limited systems, the response of plant growth to elevated CO_2 is often constrained under conditions of low nutrient availability[49–56].

Under contemporary climate conditions in dry regions, TEM generally predicts that water availability limits productivity more than nitrogen availability[8]. With a doubling of atmospheric CO_2, TEM predicts that the water-use efficiency of vegetation increases[8] in these regions; that is, there will be an increase in production per amount of water used. These predictions are consistent with research findings that increases in water-use efficiency with elevated CO_2 are generally greatest in water-stressed systems[57].

The TEM generally estimates that nitrogen limitation of NPP is much weaker in tropical forests than in temperate and boreal forests[12]. Thus, the model predicts that tropical ecosystems are able to incorporate a substantial proportion of elevated CO_2 into production. But, this result must be treated with caution because the response of tropical NPP to elevated CO_2 may be sensitive to some processes that are not presently represented in TEM; these include phosphorus limitation of NPP and C4 photosynthesis. Phosphorus-deficient soils predominate in some regions of the tropics[58] and most grasses in tropical savannas use the C4 photosynthetic pathway[59], which is generally less responsive to elevated CO_2 than C3 metabolism[57]. A substantial reduction in NPP response for tropical ecosystems would result in a much lower estimate of global NPP response to doubled CO_2.

NPP responses to changes in climate

Changes in climate with no change in CO_2 concentration are predicted to have little effect on global estimates of NPP (Table 3); the changes in NPP range from a decrease of 2.4% for the OSU climate to essentially no change for the other GCM climates (Table 3). Climate changes may affect NPP in a variety of ways. Elevated temperature may decrease NPP by decreasing soil moisture or enhancing plant respiration. It may also increase NPP by metabolically enhancing photosynthesis or increasing nutrient availability through higher rates of decomposition. In dry regions, lower precipitation or cloudiness may decrease NPP by lowering soil moisture. In moist regions, increased cloudiness may decrease NPP by reducing the availability of PAR. The relative importance of different climate variables in affecting NPP response varies among ecosystems.

For northern and temperate ecosystems, increases in NPP are generally predicted in response to climate change. For all the GCM climates, predicted temperature increases are greatest towards the poles and least in the tropics[2]. Productivity in northern and temperate ecosystems is substantially limited by nitrogen availability, and increases in productivity predicted by TEM are primarily driven by the effect of elevated temperature in enhancing the mineralization of nitrogen in the soils of these regions[8,12].

The predicted NPP decreases for tropical evergreen forest, which range between 8.9% and 20.6% among the GCM climates (Table 3), may be related to increased temperature and cloudiness. Increased temperature in TEM may enhance plant respiration enough to decrease NPP in regions where nitrogen availability does not substantially limit production[8], which is generally predicted by TEM for tropical forests[12]. Increases in cloudiness

TABLE 3 Comparison of annual NPP (10^{15} g C) by vegetation type for experiment involving two levels of atmospheric CO_2 and five levels of climate

CO_2 scenarios	312.5 p.p.m.v.					625.0 p.p.m.v.				
Climate scenarios:	Contemporary	GFDL 1	GFDL Q	GISS	OSU	Contemporary	GFDL 1	GFDL Q	GISS	OSU
Polar desert/alpine tundra	0.4	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.5
Wet/moist tundra	0.6	0.7	0.7	0.7	0.7	0.6	0.8	0.7	0.7	0.7
Boreal woodland	1.1	1.4	1.3	1.3	1.3	1.1	1.6	1.4	1.4	1.4
Boreal forest	2.9	3.8	3.6	3.6	3.5	2.9	4.4	4.0	3.7	3.7
Temperate coniferous forest	1.1	1.1	1.1	1.1	1.1	1.2	1.3	1.3	1.4	1.3
Desert	0.6	0.6	0.5	0.6	0.6	0.9	1.0	0.9	1.0	1.0
Arid shrubland	1.8	1.8	1.8	1.9	1.9	2.3	2.5	2.5	2.7	2.6
Short grassland	1.0	1.2	1.2	1.2	1.1	1.1	1.4	1.3	1.4	1.2
Tall grassland	1.2	1.4	1.4	1.5	1.3	1.3	1.5	1.5	1.6	1.4
Temperate savanna	2.2	2.3	2.4	2.6	2.4	2.5	2.9	2.9	3.1	2.9
Temperate deciduous forest	2.2	2.0	2.1	2.5	2.3	2.3	2.4	2.6	2.8	2.6
Temperate mixed forest	3.3	3.4	3.5	3.7	3.6	3.6	4.0	4.1	4.2	4.0
Temperate broadleaf evergreen forest	2.2	2.3	2.2	2.2	2.2	2.6	2.8	2.8	2.8	2.7
Mediterranean shrubland	0.5	0.5	0.5	0.5	0.5	0.6	0.6	0.6	0.7	0.6
Tropical savanna	5.3	5.7	5.6	6.0	6.0	5.6	6.3	6.3	6.7	6.6
Xeromorphic forest	2.9	2.7	2.7	2.7	2.9	3.7	3.7	3.8	3.8	4.1
Tropical deciduous forest	3.8	3.4	3.5	3.3	3.5	4.5	4.5	4.6	4.5	4.6
Tropical evergreen forest	18.0	16.4	16.3	15.6	14.3	22.0	21.9	21.8	21.3	19.3
Total	51.0	51.1	50.8	51.5	49.8	59.3	64.3	63.8	64.2	61.2

Ecosystem-based estimates may not sum to totals because of the effects of rounding in reporting those estimates.

in tropical evergreen forest may decrease PAR enough to decrease NPP[18]. The largest NPP decrease for tropical evergreen forest occurs for the OSU climate which predicts the largest increase in mean annual cloudiness (9.8%).

NPP responses to changes in CO_2 and climate

Compared to global NPP for contemporary climate at 312.5 p.p.m.v. CO_2, the global responses to changes in both CO_2 and climate do not vary substantially among the GCM climates with increases ranging between 20.0% and 26.1% (Table 3). For tropical and dry temperate ecosystems, increases in NPP are dominated by the effects of elevated CO_2. But for northern and moist temperate ecosystems, NPP increases reflect primarily the effects of elevated temperature in enhancing nitrogen availability.

Although the predicted global and ecosystem-wide responses of NPP at elevated CO_2 are generally similar for all the GCM climates, there are differences in NPP response at smaller spatial scales. For example, in eastern North America the NPP decreases just west of the Appalachian Mountains for the GFDL 1 climate (Fig. 4) may be caused by decreased precipitation. The GFDL 1 climate predicts a decrease of 7.0% in annual precipitation for temperate mixed forest in the region. In southeast Asia, the substantial NPP decreases in Indonesia for the OSU climate (Fig. 4) may be caused by increased cloudiness which reduces PAR. The OSU climate predicts an increase of 12.5% in mean annual cloudiness for tropical evergreen forest in the region.

Conclusion

The application of TEM in this study demonstrates our ability to explore, in a mechanistic manner, the potential consequences of changes in CO_2 and climate for NPP across the entire terrestrial surface of the globe. Our results indicate that simultaneous interactions among the dynamics of carbon, nitrogen, and water affect the ability of vegetation to incorporate elevated CO_2 into production. Because these interactions are both complex and spatially variable, assessments of how changes in CO_2 and climate affect NPP require the use of process-based models that are geographically referenced. The TEM represents an important tool for making these assessments because it provides scientists and policy makers with the capability to investigate the potential effects of climate change on biospheric functions in a quantitative and geographically specific way.

Although the results of this study represent our current understanding of how changes in CO_2 and climate will affect terrestrial NPP, they do not consider the redistribution of vegetation that may result from climate change. Future studies with TEM will evaluate the sensitivity of NPP to vegetation redistribution in addition to changes in CO_2 and climate. □

Received 9 November 1992; accepted 29 March 1993.

1. Watson, R. T., Filho, L. G. M., Sanhueza, E. & Janetos, A. in *Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment* (eds Houghton, J. T. *et al.*) 25–46 (Cambridge Univ. Press, Cambridge, 1992).
2. Mitchell, J. F. B., Manabe, S., Meleshko, V. & Tokioka, T. in *Climate Change: The IPCC Scientific Assessment* (eds Houghton, J. T. *et al.*) 131–172 (Cambridge Univ. Press, Cambridge, 1990).
3. Melillo, J. M., Callaghan, T. V., Woodward, F. I., Salati, E. & Sinha, S. K. in *Climate Change: The IPCC Scientific Assessment* (eds Houghton, J. T. *et al.*) 283–310 (Cambridge Univ. Press, Cambridge, 1990).
4. Agren, G. I., McMurtrie, R. E., Parton, W. J., Pastor, J. & Shugart, H. H. *Ecol. Applic.* **1,** 118–138 (1991).
5. Lieth, H. in *Primary Productivity of the Biosphere* (eds Lieth, H. & Whittaker, R. H.) 237–263 (Springer, New York, 1975).
6. Esser, G. *Tellus* **39B,** 245–260 (1987).
7. Esser, G. in *Soils and the Greenhouse Effect* (ed. Bouwman, A. F.) 249–261 (Wiley, Chichester, 1990).
8. McGuire, A. D. *et al. Clim. Change* (in the press).
9. Schimel, D. S., Parton, W. J., Kittel, T. G. F., Ojima, D. S. & Cole, C. V. *Clim. Change* **17,** 13–25 (1990).
10. Burke, I. C. *et al. BioScience* **41,** 685–692 (1991).
11. Running, S. W. & Nemani, R. R. *Clim. Change* **19,** 349–368 (1991).
12. McGuire, A. D. *et al. Globl biogeochem. Cycles* **6,** 101–124 (1992).
13. Emanuel, W. R., Shugart, H. H. & Stevenson, M. P. *Clim. Change* **7,** 29–43 (1985).
14. Prentice, K. C. *J. geophys. Res.* **95 (D8),** 11811–11830 (1990).
15. Woodward, F. I. & McKee, I. F. *Envir. Int.* **17,** 535–546 (1991).
16. Prentice, I. C. *et al. J. Biogeogr.* **19,** 117–134 (1992).
17. Smith, T. M., Leemans, R. & Shugart, H. H. *Clim. Change* **21,** 367–384 (1992).
18. Raich, J. W. *et al. Ecol. Applic.* **1,** 399–429 (1991).
19. Kimball, B. A. *Agronomy J.* **75,** 779–788 (1975).
20. Gates, D. M. in *Direct Effects of Increasing Carbon Dioxide on Vegetation, Report DOE/ER-0238* (eds Strain, B. R. & Cure, J. D.) 171–184 (US Department of Energy, Washington DC, 1985).
21. White, F. *Vegetation of Africa* (UNESCO, Paris, 1981).
22. Institute of Geography of the Siberian Department of USSR Academy of Sciences, Botanical Institute of USSR Academy of Sciences & Moscow State University Geography Department *Vegetation of the USSR* (GVGK, Minsk, 1990).
23. Hou, H. Y. *et al. Vegetation Map of China* (Map Publisher of the People's Republic of China, Beijing, 1979).

24. Matthews, E. *J. Clim. Appl. Meteorol.* **22**, 474–487 (1983).
25. Olson, J. S., Watts, J. A. & Allison, L. J. *Carbon in Live Vegetation of Major World Ecosystems, Environmental Sciences Division Publication No. 1997* (Oak Ridge National Laboratory, Oak Ridge, Tennessee, 1983).
26. Moscow State University Geographical Department *Geographical Belts and Zonal Types of the Landscapes of the World Map* (GVGK, Moscow, 1988).
27. Australian Surveying and Land Information Group *Vegetation. Atlas of Australian Resources, Third Series*, Vol. 6 (Commonwealth of Australia, Canberra, 1990).
28. Rowe, J. S. *Forest Regions of Canada Publ. 1300* (Department of Fisheries and the Environment, Can. Forest Serv., Ottawa, 1972).
29. Joint Federal-State Land Use Planning Commission for Alaska *Major Ecosystems of Alaska* (US Geological Survey, Fairbanks, Alaska, 1973).
30. Kuchler, A. W. *Potential Natural Vegetation of the Conterminous United States* (American Geographical Society, New York, New York, 1964).
31. UNESCO *Vegetation Map of South America* (UNESCO, Paris, 1981).
32. Vorosmarty, C. J. *et al. Globl biogeochem. Cycles* **3**, 241–265 (1989).
33. Deevey, E. S. Jr *Scient. Am.* **203**, 195–204 (1960).
34. Whittaker, R. H. *Communities and Ecosystems* (Macmillan, New York, 1970).
35. Olson, J. S. in *Temperate Forest Ecosystems* (ed. Reichle, D. E.) 226–241 (Springer, New York, 1970).
36. Bazilevich, N. I., Rodin, L. E. & Rozov, N. N. *Untersuchungen der Biologischen Produktivitat in Geographischer Sicht* (5th Tagung Geogr. Ges., Leningrad, 1970).
37. Study of Critical Environmental Problems (SCEP) *Man's Impact on the Global Environment* (MIT Press, Cambridge, Massachusetts, 1970).
38. Golley, F. B. in *Ecosystem Structure and Function. Ann. Biol. Colloq. 31* (ed. Wiens, J. A.) 69–70 (Oregon State University, Corvallis, Oregon, 1972).
39. Whittaker, R. H. & Likens, G. E. *Hum. Ecol.* **1**, 357–369 (1973).
40. Whittaker, R. H. & Likens, G. E. in *Primary Productivity of the Biosphere* (eds Lieth, H. & Whittaker, R. H.) 305–328 (Springer, New York, 1975).
41. Ajtay, G. L., Ketner, P. & Duvigneaud, P. in *The Global Carbon Cycle SCOPE 13* (eds Bolin, B., Degens, E. T., Kempe, S. & Ketner, P.) 129–182 (Wiley, Chichester, 1979).
42. Heimann, M. & Keeling, C. D. in *Aspects of Climate Variability in the Pacific and Western Americas, Geophysical Monograph 55* (ed. Peterson, D. H.) 237–275 (Amer. Geophys. Union, Washington DC, 1989).
43. Schlesinger, W. H. *Biogeochemistry: An Analysis of Global Change* (Academic, San Diego, California, 1991).
44. Paul, E. A. & Clark, F. E. *Soil Microbiology and Biochemistry* (Academic, San Diego, California, 1989).
45. Jenne, R. L. in *Global Climate Change: Implications, Challenges and Mitigation Measures* (eds Majumdar *et al.*) 145–164 (Pennsylvania Academy of Sciences, Easton, Pennsylvania, 1992).
46. Willmot, C. J., Rowe, C. M. & Philpot, W. D. *J. Am. Cart.* **12**, 5–16 (1985).
47. Adams, R. M. *et al. Nature* **345**, 219–224 (1990).
48. Vitousek, P. M. & Howarth, R. W. 1991. *Biogeochemistry* **13**, 87–115 (1991).
49. Wong, S. C. *Oecologia* **44**, 68–74 (1979).
50. Larigauderie, A., Hilbert, D. W. & Oechel, W. C. *Oecologia* **77**, 544–549 (1988).
51. Goudriaan, J. & de Ruiter, H. E. *Neth. J. agric. Sci.* **31**, 157–169 (1983).
52. Zangerl, A. R. & Bazzaz, F. A. *Oecologia* **62**, 412–417 (1984).
53. Brown, K. & Higginbotham, K. O. *Tree Physiol.* **2**, 223–232 (1986).
54. Oberbauer, S. F., Sionit, N., Hastings, S. J. & Oechel, W. C. *Can. J. Bot.* **64**, 2993–2998 (1986).
55. Marks, S. & Clay, K. *Oecologia* **84**, 207–214 (1990).
56. Johnson, R. H. & Lincoln, D. E. *Oecologia* **87**, 127–134 (1991).
57. Mooney, H. A., Drake, B. G., Luxmoore, R. J., Oechel, W. C. & Pitelka, L. F. *BioScience* **41**, 96–104 (1991).
58. Sanchez, P. A., Bandy, E. E., Villachica, J. H. & Nicholaides, J. J. *Science* **216**, 821–827 (1982).
59. Long, S. P. & Hutchin, P. R. *Ecol. Applic.* **1**, 139–156 (1991).

ACKNOWLEDGEMENTS. This work was primarily funded by the National Aeronautics and Space Administration. Other support came from the USDA Forest Service Resources Program and Assessment Staff, which funded A. D. McG., The National Science Foundation and the Andrew W. Mellon Foundation. D. Martin and L. Thomson of the Marine Biological Laboratory produced the colour plates. S. Mazurckiewicz of the Complex Systems Research Center assisted with processing the climate data. We thank J. D. Aber, C. Field, E. A. Griffin, A. Janetos, I. C. Prentice, J. W. Raich, C. Rosenzweig and F. I. Woodward for comments on the manuscript.