

# PRODUCTIVITY RESPONSE OF CLIMAX TEMPERATE FORESTS TO ELEVATED TEMPERATURE AND CARBON DIOXIDE: A NORTH AMERICAN COMPARISON BETWEEN TWO GLOBAL MODELS\*

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**Abstract.** We assess the appropriateness of using regression- and process-based approaches for predicting biogeochemical responses of ecosystems to global change. We applied a regression-based model, the Osnabruck Model (OBM), and a process-based model, the Terrestrial Ecosystem Model (TEM), to the historical range of temperate forests in North America in a factorial experiment with three levels of temperature (+0 °C, +2 °C, and +5 °C) and two levels of CO<sub>2</sub> (350 ppmv and 700 ppmv) at a spatial resolution of 0.5° latitude by 0.5° longitude. For contemporary climate (+0 °C, 350 ppmv), OBM and TEM estimate the total net primary productivity (NPP) for temperate forests in North America to be 2.250 and 2.602 × 10<sup>15</sup> g C · yr<sup>-1</sup>, respectively. Although the continental predictions for contemporary climate are similar, the responses of NPP to altered climates qualitatively differ; at +0 °C and 700 ppmv CO<sub>2</sub>, OBM and TEM predict median increases in NPP of 12.5% and 2.5%, respectively. The response of NPP to elevated temperature agrees most between the models in northern areas of moist temperate forest, but disagrees in southern areas and in regions of dry temperate forest. In all regions, the response to CO<sub>2</sub> is qualitatively different between the models. These differences occur, in part, because TEM includes known feedbacks between temperature and ecosystem processes that affect N availability, photosynthesis, respiration, and soil moisture. Also, it may not be appropriate to extrapolate regression-based models for climatic conditions that are not now experienced by ecosystems. The results of this study suggest that the process-based approach is able to progress beyond the limitations of the regression-based approach for predicting biogeochemical responses to global change.

## 1. Introduction

Net primary productivity (NPP) is the rate at which the vegetation in an ecosystem fixes carbon from the atmosphere (gross primary productivity) minus the rate at which it returns carbon to the atmosphere (plant respiration). As the atmospheric concentration of carbon dioxide (CO<sub>2</sub>) continues to rise (Watson *et al.*, 1992), the

NPP of terrestrial ecosystems may change in response to elevated CO<sub>2</sub>, associated changes in both temperature and precipitation, and other factors (Graham *et al.*, 1990; Bazzaz, 1990; Melillo *et al.*, 1990; Mooney *et al.*, 1991). Assessing the sensitivity of NPP to global change is important because humans rely on a portion of NPP for food, fuel, and fiber.

The results of CO<sub>2</sub>-enrichment studies suggest that NPP could increase from 25% to 50% in response to doubled CO<sub>2</sub>, given adequate nutrients and water (Kimball, 1975; Gates, 1985). In non-experimental ecosystems, where abiotic factors are not controlled, the response of productivity may be altered not only by the effects of temperature and precipitation on photosynthesis, but also by the responses of other interacting processes such as respiration, decomposition, and nutrient cycling (Kramer, 1981; Bazzaz, 1990; Melillo *et al.*, 1990; Mooney *et al.*, 1991). Because of the complexity of interactions among these processes, assessing the sensitivity of NPP to global change requires the use of models that attempt to integrate ecosystem function. Because changes in temperature and precipitation may be spatially variable (Mitchell *et al.*, 1990), estimating the response of NPP will require using models that can make geographically referenced predictions.

One type of geographically referenced model, which we define as a 'regression-based model', uses empirically derived relationships between climate and NPP to make predictions (see Agren *et al.*, 1991). Another type of model, which we define as a 'process-based model', simulates the carbon cycle by using equations that describe, in a mechanistic fashion, the transfer of carbon between different pools in an ecosystem (e.g., vegetation and soils). Although process-based models may contain some relationships that are empirical, they differ from regression-based models in that NPP depends on a number of interacting processes such as gross primary productivity, respiration, decomposition, nutrient uptake, and nutrient mineralization. Geographically referenced predictions of NPP in terrestrial ecosystems were first made with regression-based models (Lieth, 1973, 1975; Gillette and Box, 1986; Esser, 1987, 1991). Process-based models have recently been used in a geographically referenced fashion to make regional and continental predictions of NPP (Parton *et al.*, 1987; King *et al.*, 1989; Running *et al.*, 1989; Burke *et al.*, 1990, 1991; Schimel *et al.*, 1990; Raich *et al.*, 1991; Running and Nemani, 1991; McGuire *et al.*, 1992).

Both regression- and process-based models are presently available to assess the response of NPP to global change in a geographically referenced fashion. Regression-based models have been used to evaluate global carbon dynamics in response to past climatic changes (Esser, 1987, 1991). Because there is interest within the scientific community in using both regression- and process-based models for predicting biogeochemical responses to global change, questions that must be answered are: (1) Are the predicted responses similar or different between the two approaches?; and (2) How do assumptions in the approaches affect the predicted responses? In this study we address these questions by comparing NPP responses

to altered climates between a regression-based model, the Osnabruck Model (OBM; Esser, 1987, 1991), and a process-based model, the Terrestrial Ecosystem Model (TEM; Raich *et al.*, 1991; McGuire *et al.*, 1992). Both models were developed to evaluate the potential impacts of land-use, atmospheric, and climatic changes on terrestrial ecosystems. A comparison between the models should test our understanding of ecological processes at continental to global scales and at finer spatial scales. Insights gained from this comparison should advance our ability to model ecological response to global change.

We focus our comparison of the response of NPP to altered climates between OBM and TEM on temperate forests in North America. We chose these systems, in part, because of the interest in how they will be affected by global change (Pastor and Post, 1986, 1988; Solomon, 1986; Shands and Hoffman, 1987; Jarvis, 1989; Bazzaz, 1990; Graham *et al.*, 1990; Joyce *et al.*, 1990; Melillo *et al.*, 1990; Mooney *et al.*, 1991; Cook and Cole, 1991; Overpeck *et al.*, 1991). Also, the broad range of temperature and moisture conditions over which temperate forests occur provides environmental variability which can be used to examine the sensitivity of predicted NPP responses at finer spatial scales.

We apply OBM and TEM in a two-way factorial experiment with three levels of temperature increase (+0 °C, +2 °C, and +5 °C) and two levels of CO<sub>2</sub> (350 ppmv and 700 ppmv). We chose +2 °C and +5 °C because general circulation models (GCMs) generally agree that the mean surface temperature of the globe will increase between 1.5 °C and 4.5 °C with the doubling of atmospheric CO<sub>2</sub> (Mitchell *et al.*, 1990). Although GCMs generally agree that mean annual temperature will increase across the surface of the earth, the spatial distribution of changes in temperature varies from model to model (Mitchell *et al.*, 1990). Precipitation and soil moisture are expected to increase in some areas and decrease in others, and there is disagreement among the output from GCMs about the spatial distribution of these changes (Kellogg and Zhao, 1988; Mitchell *et al.*, 1990). Therefore, we do not evaluate the sensitivity of NPP response to changes in precipitation. However, besides examining the response for all temperate forests in North America, we also evaluate separately the response in moist and dry regions. This allows us to assess how assumptions in each of the models affect the response of NPP at regional and finer spatial scales, and to examine the sensitivity of response with respect to moisture availability.

## 2. Model Descriptions

### 2.1. *The Osnabruck Model (OBM)*

The OBM is a regression-based model that uses spatially referenced information on soils, climate, and land-use to estimate important carbon fluxes and pool sizes (Esser, 1987, 1991). Because there are no feedbacks between decomposition and

productivity in OBM, we need to consider only how NPP is calculated. In this study we do not use the land-use component of OBM in calculating NPP. Therefore, we apply only the NPP submodel of OBM for natural ecosystems. This submodel uses the NPP calculation of the Miami Model of Lieth (1975) which is based on regressions with annual temperature and precipitation, but has been extended to include the effects of soil fertility and CO<sub>2</sub> fertilization (Esser, 1987, 1991). Because the NPP calculated by OBM is an equilibrium prediction, the model assumes that vegetation changes in response to climatic change have been completed so that the new vegetation is in the climax condition. The OBM calculates annual NPP for a grid cell as follows (see Esser (1991) for more detail):

$$NPP = 0.475 \times \text{minimum}[NPP_T, NPP_P] \times FERT(\text{soil}) \times F(\text{CO}_2) \quad (1)$$

where 0.475 is used to convert grams of biomass to grams of carbon,  $NPP_T$  is the regression between NPP and mean annual temperature (Figure 1A),  $NPP_P$  is the regression between NPP and annual precipitation (Figure 1B),  $FERT(\text{soil})$  = soil fertility factor, a constant that depends on FAO soil type,

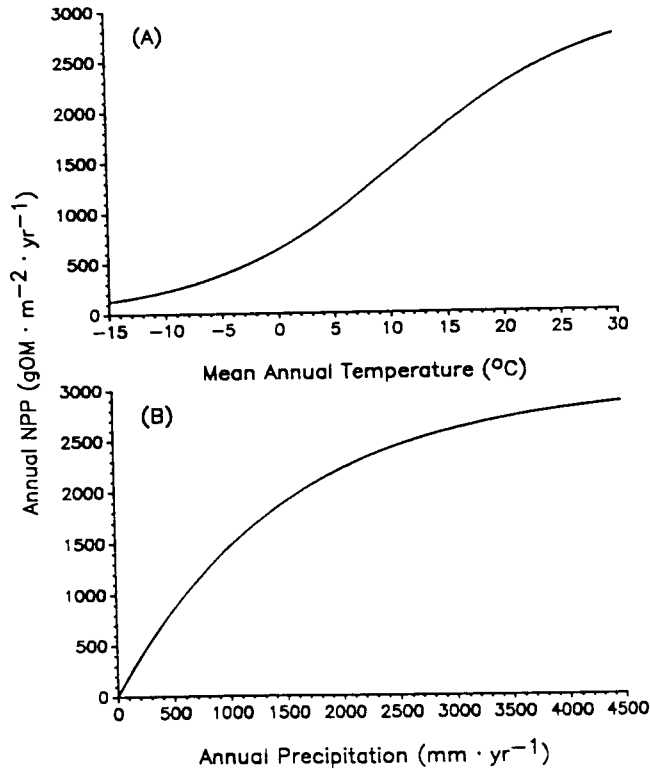


Fig. 1. The regressions in the Osnabruck Biosphere Model (OBM) between annual NPP and the independent variables of (A) mean annual temperature and (B) annual precipitation.

$$F(CO_2) = A \times (1 - e)^{-R \times (CO_2 - 80)} \quad (2)$$

$A = 1 + (FERT[soil]/4)$ ,  $R = -\ln([A - 1]/A)/240$ , and  $CO_2$  = atmospheric concentration of  $CO_2$  in ppmv. The functions  $NPP_T$ ,  $NPP_P$ , and  $F(CO_2)$  monotonically saturate with increasing temperature, precipitation, and carbon dioxide, respectively. Although both  $NPP_T$  and  $NPP_P$  saturate at  $3000 \text{ g organic matter} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , the former is logistic in shape whereas the latter is a saturating exponential function. The function  $F(CO_2)$ , which is similar in shape to  $NPP_P$ , saturates at the value of  $A$ . For a given level of  $CO_2$ ,  $F(CO_2)$  will be higher for soils with higher fertility.

## 2.2. The Terrestrial Ecosystem Model (TEM)

The TEM uses spatially referenced information on climate, soils, and vegetation to make monthly estimates of important carbon (C) and nitrogen (N) fluxes and pool sizes. The first two versions of TEM consisted of five pools and nine fluxes (Raich *et al.*, 1991; McGuire *et al.*, 1992). For this study we enhance TEM to model the recycling of N within the vegetation so that the simulated transient response of NPP to a step function of elevated  $CO_2$  is consistent with experimental observations in nutrient-limited systems (Wong, 1979; Goudriaan and de Ruiter, 1983; Zangerl and Bazzaz, 1984; Brown and Higginbotham, 1986; Oechel and Riechers, 1986; Tissue and Oechel, 1987). These observations indicate that NPP in a nutrient-limited system should first increase and then decline to a value that is greater than or equal to the initial level. To implement the recycling of N within the vegetation, we altered the structure of TEM by splitting the vegetation N pool into structural and labile pools (Figure 2). We also added two fluxes that transfer N between these pools and split the total N uptake flux into structural and labile components.

For each time step in a model run,  $NPP$  is calculated as the difference between gross primary productivity ( $GPP$ ) and plant respiration ( $R_A$ ). The flux  $GPP$  is calculated at each time step as follows:

$$GPP = C_{\max} \times f(PAR) \times f(LEAF) \times f(T) \times f(CO_2, H_2O) \times f(NA) \quad (3)$$

where  $C_{\max}$  is the maximum rate of C assimilation,  $PAR$  is photosynthetically active radiation,  $LEAF$  (i.e., leaf phenology) is leaf area relative to maximum annual leaf area.  $T$  is temperature, and  $NA$  is N availability. The parameter  $C_{\max}$ , which is in units of  $\text{g C} \cdot \text{m}^{-2} \cdot \text{month}^{-1}$ , was calibrated to be 1014, 1126, and 1208 for temperate conifer, mixed, and deciduous forests, respectively. The functions  $f(PAR)$  and  $f(LEAF)$  are described in Raich *et al.* (1991). The function  $f(T)$ , which is described in McGuire *et al.* (1992), is a parabolic function that rises from 0 to 1 between the minimum and optimum temperatures of photosynthesis for each vegetation type and remains at 1 above the optimum temperature (Figure 3A). The function  $f(CO_2, H_2O)$  is hyperbolic with respect to the concentration of  $CO_2$  within leaves of the canopy (Figure 3B). This concentration is the product of ambient  $CO_2$  concentration and relative canopy conductance to  $CO_2$ , which is

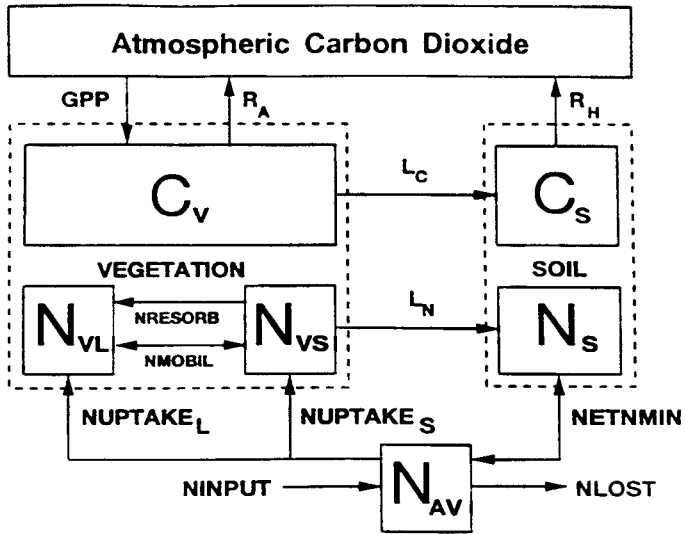


Fig. 2. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation ( $C_V$ ); structural nitrogen in the vegetation ( $N_{VS}$ ); labile nitrogen in the vegetation ( $N_{VL}$ ); organic carbon in soils and detritus ( $C_S$ ); organic nitrogen in soils and detritus ( $N_S$ ); and available soil inorganic ( $N_{AV}$ ). Arrows show carbon and nitrogen fluxes:  $GPP$ , gross primary productivity;  $R_A$ , autotrophic respiration;  $R_H$ , heterotrophic respiration;  $L_C$ , litterfall C;  $L_N$ , litterfall N;  $NUPTAKE_S$ , N uptake into the structural N pool of the vegetation;  $NUPTAKE_L$ , N uptake into the labile N pool of the vegetation;  $N_{RESORB}$ , N resorption from dying tissue into the labile N pool of the vegetation;  $N_{MOBIL}$ , mobilized between the structural and labile N pools of the vegetation;  $NETNMIN$ , net N mineralization of soil organic N;  $N_{INPUT}$ , N inputs from outside the ecosystem; and  $N_{LOST}$ , N losses from ecosystem.

positively related to water availability (Raich *et al.*, 1991; McGuire *et al.*, 1992). The half-saturation constant of  $f(CO_2, H_2O)$  has been chosen to increase the function by 37% for a doubling of atmospheric  $CO_2$  from 340 ppmv to 680 ppmv given no water limitation (McGuire *et al.*, 1992). Among studies that provide adequate nutrients and water to plants, the range in the response of plant growth to doubled  $CO_2$  is between 25% and 50% (Kimball, 1975; Gates, 1985).

The function  $f(NA)$ , which was first introduced in McGuire *et al.* (1992), models the effects of N supply on GPP. It is less than 1 when N supply, defined as the combination of N uptake and vegetation labile N, limits the construction of new tissue. Thus, C uptake is constrained when N supply limits production; an analogous function constrains N uptake when C supply limits production. We make use of information on the C to N ratio of production ( $P_{cn}$ ), a quantity commonly measured in ecosystem studies, to determine when N supply limits production:  $f(NA)$  is adjusted so that production has a C to N ratio equal to  $P_{cn}$ . Thus, this implementation assumes that nitrogen use efficiency, defined as the ratio of NPP to N in new production, is conservative within a vegetation type. The parameter  $P_{cn}$  is higher for coniferous forests than for deciduous forests, although there is some flexibility within each of the forest types (McGuire *et al.*, 1992).

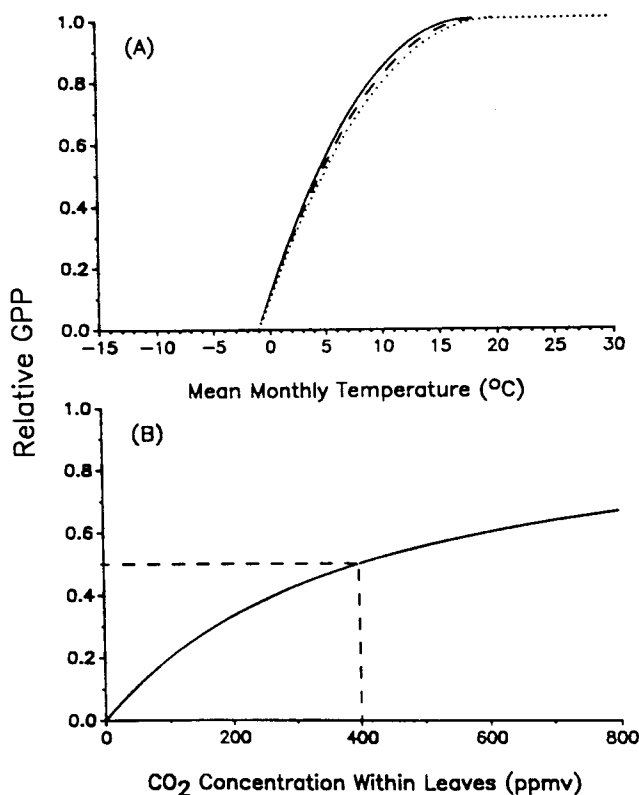


Fig. 3. The relationships in the Terrestrial Ecosystem Model (TEM) between relative gross primary productivity (GPP) and the independent variables of (A) mean monthly temperature and (B) the concentration of CO<sub>2</sub> within leaves. The temperature relationship is defined to saturate at 18 °C, 19 °C, and 20 °C for temperate conifer (solid line), mixed (dashed line), and deciduous (dotted line) forests, respectively. In the CO<sub>2</sub> relationship, the half-saturation constant of 400 ppmv was chosen to increase the function by 37% for a doubling of atmospheric CO<sub>2</sub> from 340 ppmv to 680 ppmv given no water limitation.

In TEM,  $R_A$  at each time step is the sum of maintenance respiration and growth respiration. Maintenance respiration ( $R_m$ ) is calculated at each time step as follows:

$$R_m = K_r \times C_v \times e^{r_T \times T} \quad (4)$$

where  $K_r$  is the per-gram-biomass respiration rate of the vegetation at 0 °C,  $C_v$  is the mass of carbon in the vegetation,  $T$  is the mean monthly air temperature, and  $r_T$  is the instantaneous rate of change in respiration. As described in McGuire *et al.* (1992),  $r_T = \ln(Q_{10})/10$  where  $Q_{10} = 2.35665 - (0.05308 \times T) + (0.00238 \times T^2) - (0.00004 \times T^3)$ . Growth respiration ( $R_g$ ) is calculated to be 25% of C in production for  $NPP$  greater than 0. For time steps when  $NPP$  is less than 0, i.e.,  $R_m$  greater than  $GPP$ ,  $R_g$  is calculated to be 0.

To make an estimate of NPP in TEM, the model is run for a grid cell until all fluxes are in steady state; in this study, the model was run with N inputs and losses set to 0. Because the NPP calculated by TEM is an equilibrium solution, the prediction corresponds to vegetation in the climax condition. The spatial extrapolation of TEM is accomplished by running the model for each grid cell in a region. This procedure requires the use of the monthly climatic data and the soil- and vegetation-specific parameters appropriate to the grid cell. Although many of the vegetation-specific parameters in the model are defined from published information, some are determined by calibrating the model to the steady state fluxes and pool sizes of an intensively studied field site, the calibration site for the ecosystem. For each of the vegetation types in this study, we calibrated TEM to the same equilibrium fluxes and pool sizes used in the respective calibrations of McGuire *et al.* (1992).

### 3. Data Used for Spatially Extrapolating the Models

To make an estimate for a grid cell, OBM requires climatic and soil data for the grid cell whereas TEM additionally requires data on vegetation. The temperature and precipitation data sets for the +0 °C treatments in the experiment were derived from the global data sets of Legates and Willmott (1988) which are organized at spatial resolution of 0.5° latitude by 0.5° longitude. For the elevated-temperature treatments we added either +2 °C or +5 °C to each mean monthly temperature in the temperature data set. Mean annual temperature was determined by summing the monthly temperature values and dividing by 12. Annual precipitation was determined by summing the monthly values in the precipitation data set. The annual data sets were used by OBM to calculate NPP for the various treatments in the experiment. In each of the models, CO<sub>2</sub> was set to either 350 ppmv or 700 ppmv depending on treatment. For TEM, the monthly temperature and precipitation data sets were used and CO<sub>2</sub> did not vary seasonally.

The soil data set used by both OBM and TEM was derived from the digitization (0.5° latitude by 0.5° longitude resolution) of the FAO-UNESCO (1971) soil map. The soil fertility factor of OBM was determined for each soil type from Table 3 of Esser (1991). For those soil types that are not in the table we assumed  $FERT(soil)$  to be 1.

The TEM uses hydrologic data sets that depend on interactions between temperature, precipitation, and irradiance. The Water Balance Model (WBM) of Vorosmarty *et al.* (1989) with refinements by Rastetter (pers. comm.) was used to produce estimates of potential evapotranspiration, actual evapotranspiration, and soil moisture for TEM. The WBM was run with the appropriate temperature information to produce these data sets for the different treatments of the experiment. In all cases, WBM used the cloudiness data set of Hahn *et al.* (1988) to determine irradiance. This data set was also used by TEM to calculate photosynthetic active radiation.



We defined the historical range of temperate forest in North America by the ranges of temperate conifer forest, temperate deciduous forest, and temperate mixed forest in the vegetation used by McGuire *et al.* (1992). The 1826 grid cells (0.5° latitude by 0.5° longitude resolution) that define this region cover about 20% of the continent (Figure 4).

#### 4. Approach to Model Comparisons

We consider the +0 °C and 350 ppmv CO<sub>2</sub> combination of the experiment to be 'contemporary climate' and use the NPP predictions in this treatment as the reference for NPP responses to altered climates. Therefore, we first compare the NPP predictions between the two models for contemporary climate. We then compare the responses of NPP to altered climates by considering separately the responses to elevated temperature only, elevated CO<sub>2</sub> only, and both elevated temperature and CO<sub>2</sub>. In addition to examining responses for the entire range of temperate forest we also analyze responses in both moist and dry regions of temperate forest.

To examine interactions between elevated temperature and CO<sub>2</sub> in moist regions of temperate forest, we chose a north-south transect at 82.0° W located between 46.0° N in southern Canada and 28.0° N in central Florida (Figure 4). The transect crosses the Appalachian Mountains between latitudes 37.0° N and 35.0° N. Along the transect, mean annual temperature increases from less than 5 °C at the northern end to over 20 °C at the southern end (Figure 5). Annual precipitation along the transect increases from about 900 mm at the northern end to about 1400 mm at the southern end (Figure 5). Both models make estimates for 30 grid cells along this transect; estimates are not made for five grid cells that cross Lake Huron and two that cross Lake Erie.

North of 35.5° N the transect is classified as temperate deciduous forest. The remainder of the transect is classified as temperate mixed forest. In the southern portion of the transect, a number of grid cells have gleyic soils (Figure 4), and are considered by TEM as soils that are poorly drained. These grid cells are treated by TEM as if moisture is not limiting, i.e., soil moisture is set to field capacity and estimated evapotranspiration is set to potential evapotranspiration. The grid cells with gleyic soils occur at the following latitudes: 28.0° N, 29.5° N–32.0° N, and 33.0° N.

To examine interactions between elevated temperature and CO<sub>2</sub> in dry regions of temperate forest, we chose all the temperate forest grid cells that occur in a quadrangle between latitudes 28.5° N and 35.0° N and between longitudes 105.0° W and 115.0° W (Figure 4). This region includes a portion of northern Mexico and much of the states of New Mexico and Arizona. The 30 temperate forest grid cells that occur in this region are classified as temperate conifer forest. For these grid cells, total annual precipitation varies from 280 mm to 649 mm and mean annual temperature varies from 8.9 °C to 22.0 °C.

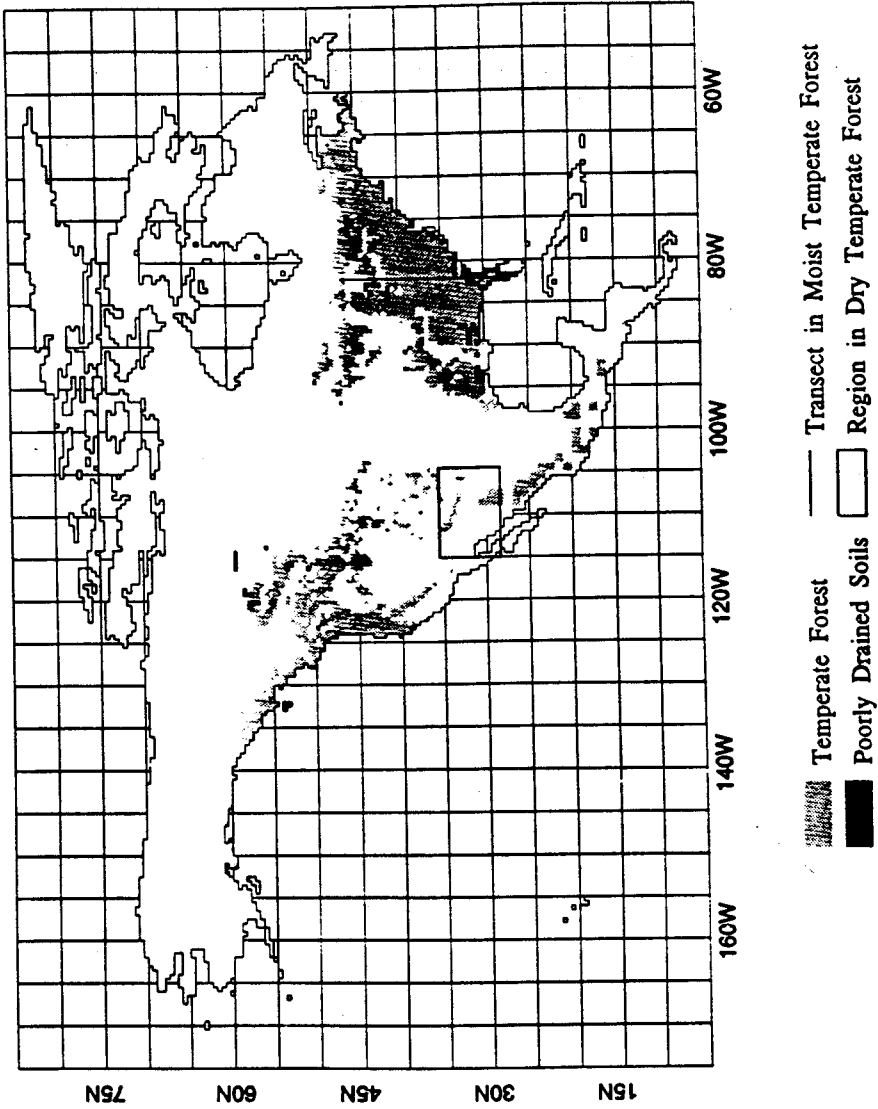


Fig. 4. The historical range of temperate forest in North America (light shading) as defined by this study at a spatial resolution of 0.5° latitude by 0.5° longitude. The dark shading indicates the range of poorly drained soils within the range of temperate forest. The transect in eastern North America and the quadrangle in the southwest United States are used to examine the responses of NPP as they are affected by elevated temperature and CO<sub>2</sub> in moist and dry regions of temperate forest, respectively.

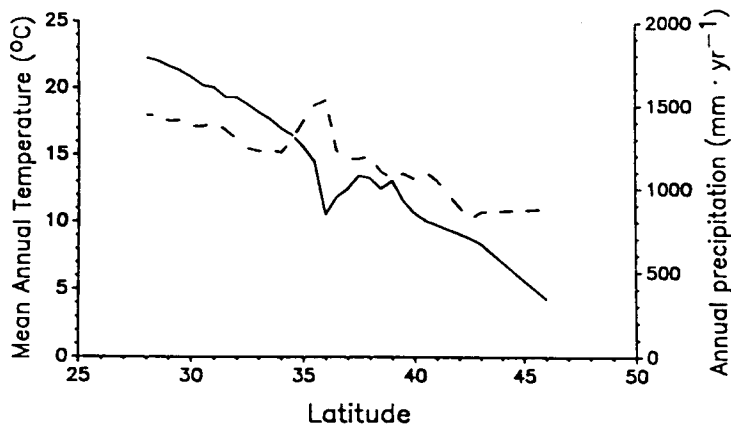


Fig. 5. Mean annual temperature (solid line) and total annual precipitation (dashed line) for grid cells on a north-south transect at 82.0° W.

## 5. Results

### 5.1. Comparison of Estimates for Contemporary Climate

For the contemporary climate scenario (+0 °C, 350 ppmv CO<sub>2</sub>), OBM and TEM estimate the annual NPP for climax temperate forests in North America to be 2.250 and 2.602 × 10<sup>15</sup> g C · yr<sup>-1</sup> (534.6 and 618.3 g C · m<sup>-2</sup> · yr<sup>-1</sup>), respectively (Table I). Because of uncertainties in field estimates of NPP, the models can be considered to make similar continental-scale estimates of the exchange of carbon between temperate forests and the atmosphere. However, there are substantial differences between the models' estimates at regional and finer spatial scales (Figure 6, Table I).

For deciduous and mixed forests, which occur mostly in eastern North America,

TABLE I: Comparison between the Osnabruck Model (OBM) and the Terrestrial Ecosystem Model (TEM) of estimated annual net primary productivity (NPP) for undisturbed climax temperate forests in North America

Ecozone	Area 10 <sup>6</sup> km <sup>2</sup>	Cells 0.5°	Total NPP 10 <sup>15</sup> g C · yr <sup>-1</sup>	Max NPP g C · m <sup>-2</sup> · yr <sup>-1</sup>	Min NPP
Temperate conifer forest	1.51	693	OBM: 0.761	1598.4	66.2
			TEM: 0.625	669.9	205.3
Temperate deciduous forest	0.90	376	OBM: 0.574	2047.5	197.3
			TEM: 0.675	980.2	411.4
Temperate mixed forest	1.80	757	OBM: 0.915	2669.9	154.6
			TEM: 1.302	1038.7	401.5
All temperate forests	4.21	1826	OBM: 2.250	2669.9	66.2
			TEM: 2.602	1038.7	205.3

