

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 CO₂ (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 × 10¹⁵ g C · yr⁻¹, 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 CO₂, 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 CO₂ 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 (CO₂) continues to rise (Watson *et al.*, 1992), the

NPP of terrestrial ecosystems may change in response to elevated CO₂, 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 CO₂-enrichment studies suggest that NPP could increase from 25% to 50% in response to doubled CO₂, 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 CO₂ (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 CO₂ (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 CO₂ 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,

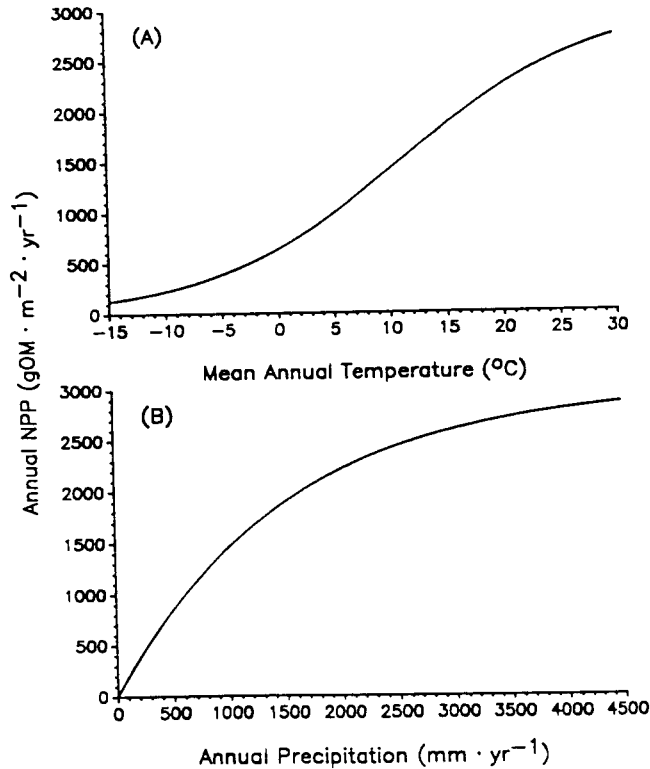


Fig. 1. The regressions in the Osnabruck Biosphere Model (OBM) between annual NPP and the independent variables of (A) mean annual temperature and (B) annual precipitation.

$$F(\text{CO}_2) = A \times (1 - e)^{-R \times (\text{CO}_2 - 80)} \quad (2)$$

$A = 1 + (\text{FERT}[\text{soil}]/4)$, $R = -\ln([A - 1]/A)/240$, and CO_2 = atmospheric concentration of CO_2 in ppmv. The functions NPP_T , NPP_P , and $F(\text{CO}_2)$ 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 $F(\text{CO}_2)$, which is similar in shape to NPP_P , saturates at the value of A . For a given level of CO_2 , $F(\text{CO}_2)$ 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:

$$GPP = C_{\max} \times f(PAR) \times f(LEAF) \times f(T) \times f(\text{CO}_2, \text{H}_2\text{O}) \times f(NA) \quad (3)$$

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 $f(\text{CO}_2, \text{H}_2\text{O})$ 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

