11. Regional Impacts of Climate Change and Elevated Carbon Dioxide on Forest Productivity

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Net primary production (NPP) is defined as the rate at which carbon (C) is accumulated by autotrophs and is expressed as the difference between gross photosynthesis and autotrophic respiration. NPP is the resource providing for the growth and reproduction of all heterotrophs on Earth; as a result, it determines the planet's carrying capacity (Vitousek et al., 1986). For humans, terrestrial NPP is important because it is one determinant of the available food and wood supplies, and because it drives the rates of most other processes identified as "ecosystem services" provided by terrestrial systems (Costanza et al., 1997; Daily et al., 1997). Forests store 90% of the C in terrestrial vegetation (Graham et al., 1990), so fluxes of C between forest biomass, forest soils, and the atmosphere are key components of global and regional C budgets. In the northeastern U.S., forest production is especially important because nearly 70% of the land area in the region is forested (Lathrop and Bognar, 1994).

NPP depends on the balance between rates of photosynthesis and respiration, both of which are sensitive to changing environmental conditions. As a result, terrestrial NPP is likely to change dramatically in a future marked by increasing carbon dioxide (CO_2) concentrations and greenhouse gas-induced climate change. In this chapter we first compare

results from two ecosystem process models, PnET-II (Aber and Federer, 1992; Aber et al., 1995, 1996) and TEM 4.0 (Raich et al., 1991; McGuire et al., 1992, 1993; Melillo et al., 1993), which are driven by scenarios of potential future climate in order to predict forest productivity in the northeastern region under changing environmental conditions. We highlight those features of the models and input data sets that contribute to differences between model predictions. We then describe state-of-the-art methods to address issues not usually considered when developing regional estimates of forest NPP. Consideration of these additional issues will enable more accurate predictions of forest NPP for the region.

Carbon Dioxide, Climate Change, and Forest Productivity

Atmospheric CO_2 concentrations have increased by nearly 30% over the last 200 years, primarily as a result of fossil fuel combustion, land use change, and cement production (Neftel et al., 1985; Vitousek, 1992; Schimel et al., 1996a). If emissions continue to climb at this rate, a doubling of atmospheric CO_2 is possible by 2100, though the adoption of mitigation strategies may slow the growth rate or stabilize CO_2 concentrations (Houghton, 1996). Also within the last two centuries, atmospheric concentrations of gases such as tropospheric ozone (O_3), methane (CH_4), and nitrous oxide (N_2O) have increased as a result of human activity. There is substantial evidence that together with CO_2, these greenhouse gases have contributed to a global surface temperature warming of 0.3 to 0.6°C over the last century, with 0.2 to 0.3°C of this warming occurring within the last 40 years (Nicholls et al., 1996; Schimel et al., 1996a). The recent greenhouse-gas–induced warming has been greatest in the northern latitudes, from 40 to 70°N (Nicholls et al., 1996) including the northeastern region of the U.S. discussed in this chapter (lat 41 to 47.5°N, long 67 to 76°W). Future temperature changes are expected to be most dramatic toward the poles (Kattenberg et al., 1996). While most climate models predict an increase in global mean precipitation, there is little agreement about precipitation trends at the regional level (Kattenberg et al., 1996). A useful review of the sources and dynamics of greenhouse gases, and of the specific changes in climate that may result from their emissions, can be found in the report of the Intergovernmental Panel on Climate Change (Houghton et al., 1996).

The physiological responses of plants to increased CO_2 and climate change have been the subject of hundreds of publications within the past several decades. Although a detailed review of the literature on this topic is beyond the scope of this chapter, some recent discussions can be found in Strain (1987), Eamus and Jarvis (1989), Bazzaz (1990), Graham et al. (1990), Mooney et al. (1991), Bazzaz and Fajer (1992), Mousseau and

Saugier (1992), Idso and Idso (1994), Bazzaz et al. (1996), Koch and Mooney (1996), Körner (1996), Wilsey (1996), and Navas (1998). Overall, increased CO_2 is thought to have a direct effect on stomatal function and carboxylation rates, changing photosynthesis and transpiration (Jarvis and McNaughton, 1986; Field et al., 1995). Increased CO_2 has been shown to impact respiration rates as well, though the direction of change appears to vary (Amthor, 1991). At the same time climate changes, which are projected to be indirect effects of CO_2 and greenhouse-gas increases, are likely to alter the rates of respiration, decomposition, and nutrient cycling in addition to photosynthesis and transpiration. Thus at the whole-ecosystem level, complex interactions between the vegetation CO_2 response, biogeochemical cycles, and water and energy fluxes are likely. The complexity of these interactions makes it difficult to extrapolate from short-term physiological measurements to prediction of long-term system responses (Mooney, 1996).

While much progress has been made toward quantifying forest response to elevated CO_2 using short-term physiological measurements, data are becoming available that illustrate potential shortcomings of the approaches used to date. For example, in addition to affecting photosynthesis, studies by Zak et al. (1993), Wood et al. (1994), Cotrufo and Ineson (1996), and Randlett et al. (1996) have shown that enhanced CO_2 and climate change can impact allocation, foliar composition, decomposition, and nutrient cycling. Bazzaz et al. (1996) have pointed out the potential danger of extrapolating from seedling experiments to mature tree responses. Eamus (1991) has suggested that transporting plants grown at ambient CO_2 directly to increased-CO_2 environments can induce potentially unrealistic physiological responses. Few researchers have explored plant acclimation or evolutionary response to elevated CO_2 although this possibility has been acknowledged in several studies (e.g., Sage et al., 1989; Field et al., 1995; Bazzaz et al., 1996). Bolker et al. (1995), Körner (1996), Lüscher and Nösberger (1997), and Lüscher et al. (1998) have suggested that shifts in competitive interactions under increased CO_2 and climate change are likely to induce species changes, which may impact stand- and regional-scale photosynthetic rates. Finally, several modeling studies (e.g., Rastetter et al., 1991, 1992; McGuire et al., 1992, 1997; Melillo et al., 1993) have highlighted potential effects of nutrient availability on long-term photosynthetic response. Free-Air CO_2 Enrichment (FACE) experiments, in which mature stands are exposed to elevated CO_2 concentrations, are a promising alternative to greenhouse and pot experiments, but currently they are limited by technological and cost constraints and they sample only a small portion of a tree's life span (Bazzaz et al., 1996). Still, results from FACE studies conducted in forests suggest that substantial increases in photosynthesis and NPP are possible (Ellsworth et al., 1995; DeLucia et al., 1999), though long-term acclimation to elevated CO_2 remains a possibility.

In the forest ecosystems of the northeastern U.S., additional factors are thought to influence productivity, such as increasing tropospheric O_3 concentrations (Ollinger et al., 1997), acid rain and cation depletion (Likens et al., 1996), and nitrogen (N) deposition (Ollinger et al., 1993; Lovett, 1994; Townsend et al., 1996), but see also Nadelhoffer et al. (1999). Under a changed climate, the frequencies of disturbances such as fire and pathogen outbreaks are also likely to change, further altering productivity patterns (Schimel et al., 1997). An attempt at accurate and complete prediction of future forest NPP in the northeastern U.S. would require consideration of each of these separate, yet potentially interacting, factors. In this chapter, our intent is not to attempt an integrated assessment of forest response to all of the stressors that affect forest productivity in the region. Such an assessment would be premature given the current state of knowledge about the interactions between these factors. Instead, we focus on the potential impacts of enhanced CO_2 and climate change on forest productivity in the northeastern U.S. We anticipate that eventually, future research will examine the integrated responses of forests to these many stressors.

Modeling Forest Productivity

Because the NPP response of forests to the interacting factors discussed above is likely to be extremely complex, single-factor experiments to determine how intact systems will respond to future perturbations are necessarily limited in their predictive ability. The inevitable shortcomings of past experimental approaches in assessing the long-term impacts of increased CO_2 on plant production make it very difficult to use an experimental approach to measure plant response to elevated CO_2, which is just one of several stressors likely to be important in the future.

When experimental measurements are difficult or impossible, models can be useful predictive tools. A modeling approach may be used to extrapolate process descriptions from site-level measurements to regional-scale estimates (Aber et al., 1993a). Models may also be used to predict forest response to conditions that do not yet exist, such as the likely convergence of several interacting stressors in the northeastern U.S. under a changed climate and increased atmospheric CO_2. Of course, uncertainty always exists in model estimates (Oreskes et al., 1994), and it is impossible to validate predictions of the future (Rastetter, 1996). However, it is to our advantage to present our best predictions, basing those estimates on models parameterized using existing data.

Many different modeling approaches have been used to develop regional to global estimates of NPP to fulfill a variety of objectives (e.g., Cramer et al., 1999). Some models estimate NPP across the globe based on general empirical relationships of NPP with temperature, precipitation,

or NDVI, whereas other models estimate NPP across a limited region based on very detailed information, such as the types of tree species found in the region or the division of vegetation into many compartments (e.g., leaves, sapwood, heartwood, fine roots). Because our understanding of ecosystem dynamics is imperfect, different models may highlight the influences of different environmental factors or feedback mechanisms on NPP (e.g., Churkina et al., 1999; Ruimy et al., 1999; Schloss et al., 1999). These differences in model structure and assumptions may or may not be important when determining regional NPP estimates or the influence of enhanced CO_2 and climate change on future forest productivity. A comparison of model estimates against field-measured data can provide useful information about model accuracy under current conditions (Aber, 1997). However, models can estimate very different NPP responses to future climate change even though they may estimate similar NPP under current conditions (VEMAP Members, 1995). Comparisons between results generated by models with different underlying principles may help to indicate what differences in model assumptions are important. These differences then suggest lines for further inquiry and point to areas where more experimental data are needed.

In this chapter, we compare the NPP responses of forests in the northeastern U.S. to enhanced CO_2 and climate change as simulated by two models that were developed for very different purposes: PnET-II and version 4.0 of the Terrestrial Ecosystem Model (TEM). PnET-II is an uncalibrated, monthly time-step C and water balance model built around generalized physiological relationships. The PnET suite of models has been used to examine the influence of N deposition, climate change, O_3 exposure, and land use history on nutrient cycling and forest production in the northeastern and southeastern U.S. and Ireland. The Terrestrial Ecosystem Model is a highly aggregated process-based ecosystem model that has been developed to examine the monthly C, N, and water dynamics within terrestrial ecosystems across the globe.

Model Descriptions

PnET-II

In PnET-II (Fig. 11.1a), aboveground vegetation C is stored in four compartments (Aber and Federer, 1992; Aber et al., 1995): foliar canopy, plant (mobile) C, bud C, and wood. Atmospheric CO_2 is taken up by the canopy during photosynthesis and C is either respired or allocated to the various compartments.

A multilayered forest canopy is constructed in which available light and specific leaf weight decline with canopy depth. Light attenuation through the canopy is based on the Beers–Lambert exponential decay equation ($y = e^{-k*LAI}$). Maximum gross photosynthesis is calculated individually

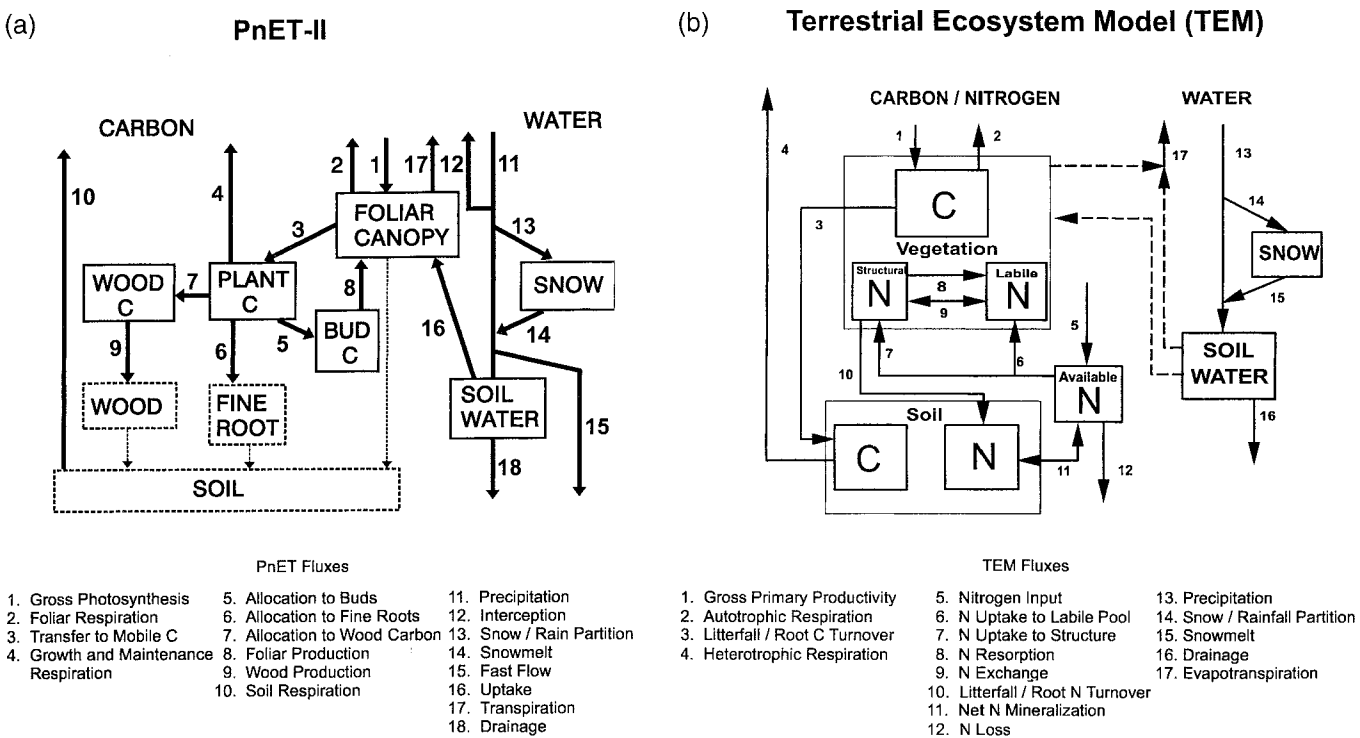


Figure 11.1. Schematic of model structures of (a) PnET-II and (b) Terrestrial Ecosystem Model (TEM) version 4.0.

for each of the 50 canopy layers in order to capture the effect of gradual light extinction on C gain. For each layer, gross photosynthesis is a function of the predicted maximum photosynthetic rate attenuated by environmental conditions, such as water availability, temperature, and daylength. Maximum photosynthetic rate is determined as a linear function of foliar N content, following the observed relationship between these two variables across species from diverse ecosystems (Field and Mooney, 1986; Reich et al., 1995). Net photosynthesis is calculated by subtracting day and night foliar respiration from gross photosynthesis. After the newly acquired C has been allocated to the wood C, plant C, and bud C compartments, NPP is calculated as the sum of wood production, foliar production, and the allocation of C to fine roots (see Fig. 11.1a).

Stomatal conductance is directly related to net photosynthetic rate, making water use efficiency (WUE) a function of vapor pressure deficit (VPD) (Tanner and Sinclair, 1983; Sinclair et al., 1984). In this way, transpiration can be predicted from canopy photosynthesis and VPD, providing a direct link between the C and water balance portions of the model. The long-term sustainability of increases in photosynthetic rate as a result of enhanced ambient CO_2 is uncertain, due to the possibility of acclimation or nutrient limitation (Bazzaz, 1990; Rastetter et al., 1991). Therefore, the atmospheric CO_2 increase is assumed to have direct effects on WUE and not on photosynthetic rate. Using PnET-II for the northeastern U.S., a doubling of CO_2 is assumed to result in a doubling of WUE (Aber et al., 1995).

While PnET-II does not calculate a complete soil C budget, it does predict some transfers between above- and belowground pools. For example, C is transferred from the mobile plant pool to roots and wood, and soil respiration (which includes both microbial and root respiration) (Aber et al., 1995) draws on the C assumed to exist belowground (see Fig. 11.1). Net ecosystem productivity (NEP) is calculated on a monthly basis as the difference between net photosynthesis and the sum of four respiration terms: foliar growth respiration, wood maintenance respiration, wood growth respiration, and soil respiration (see Fig. 11.1a). Computationally, the energy source for the aboveground vegetation respiration terms is the mobile C pool. The monthly NEP values are summed for a yearly NEP prediction.

Parameters in PnET-II are obtained on a regional basis from field data, and are not calibrated to make model results match measured output data. The model has performed well at predicting forest production and runoff at diverse locations across North America (Aber and Federer, 1992; Aber et al., 1995), and has been tested against eddy correlation CO_2 exchange measurements (Aber et al., 1996). To date, the PnET models have been applied to forests in the northeastern U.S. at spatial resolutions of 60 arcseconds (60″) (approximately 1.5 km) and 0.5° (approximately 40 to 50 km) (Aber et al., 1995, 1997; Ollinger et al., 1997, 1998; Jenkins et al.,

1999), to forests in the southeastern U.S. at spatial resolution of 0.5° (McNulty et al., 1996), and to forests in Ireland at a spatial resolution of 1 km (Goodale et al., 1997).

Terrestrial Ecosystem Model 4.0 (TEM 4.0)

Unlike PnET-II, vegetation C (both aboveground and belowground) in TEM 4.0 is simulated as a single compartment (Raich et al., 1991). Atmospheric CO_2 is taken up by plants through gross primary productivity (GPP) and C is then respired back to the atmosphere, retained as vegetation C, or transferred to the soil C compartment as litterfall (see Fig. 11.1b).

Monthly GPP is influenced by photosynthetically active radiation (PAR), leaf area, air temperatures, actual evapotranspiration, potential evapotranspiration, N availability, and atmospheric CO_2 concentration (Raich et al., 1991; McGuire et al., 1992, 1993, 1995, 1997). Monthly plant respiration depends on air temperature and vegetation C (Raich et al., 1991). NPP is calculated as the difference between GPP and plant respiration (see Fig. 11.1b).

The relationship between C assimilation and intercellular CO_2 is described by empirical functions representing limits imposed by carboxylation, light availability, synthesis, and N availability (Wullschleger, 1993; Sage, 1994; McGuire et al., 1997). Intercellular CO_2 is determined from atmospheric CO_2 by a canopy conductance term which depends on water availability (McGuire et al., 1997). For simulations of the effects of increased atmospheric CO_2 in this study, ambient CO_2 was doubled from 355 to 710 ppmv.

TEM 4.0 includes decomposition and N dynamics in its predictions. Nitrogen availability, which is determined by predicted N mineralization rate, can limit photosynthesis and NPP (McGuire et al., 1997; Pan et al., 1998; Kicklighter et al., 1999). Litterfall and root turnover are simulated as transfers from vegetation to soil C and N pools, and N is transferred between the soil N pool and the available N pool via N mineralization. In this way, N availability depends on the recycling of N from decomposing litter and soil organic matter so that rates of NPP are coupled to rates of decomposition. Thus, changes in N availability caused by climate change may also influence future NPP estimates. NEP is calculated monthly as the difference between GPP, autotrophic respiration (growth and maintenance respiration by all plant parts), and heterotrophic respiration (respiration by belowground microbes).

Although many of the vegetation-specific parameters in TEM 4.0 are defined from published information (Raich et al., 1991; McGuire et al., 1992; Melillo et al., 1993), some are determined on a biome-specific basis by calibrating the model to the fluxes and pool sizes of intensively studied field sites. To date, TEM has been applied using data sets gridded at

a resolution of 0.5° latitude by 0.5° longitude for South America (Raich et al., 1991), North America (McGuire et al., 1992, 1993; VEMAP Members, 1995), and the globe (Melillo et al., 1993; McGuire et al., 1997; Xiao et al., 1997).

Equilibrium Assumptions

PnET-II and TEM 4.0 are applied in the first section of the chapter as equilibrium models. This means that they simulate a future in which CO_2 concentrations and climate have stabilized and vegetation distribution is constant. They do not include the effects of events such as changes in disturbance frequencies, reduction of C stored in biomass, changing vegetation distributions, or altered soil water-holding capacity (WHC) as a result of changing climate (Pastor and Post, 1988, 1993; Smith and Shugart, 1993). While there is growing recognition that these transient processes are potentially very important during the process of climate change (for example, see Tian et al., 1999), at present there is little consensus about the direction or magnitude of the transient responses (Melillo et al., 1996), especially at the regional level.

Influence of Model Assumptions on Net Primary Production Estimates

A comparison of the structures and assumptions of PnET-II and TEM 4.0 suggests two issues to be examined in this study. First, how does the representation of above- and belowground processes affect model predictions of NPP under enhanced CO_2 and climate change? In PnET-II (Aber and Federer, 1992; Aber et al., 1995, 1996), aboveground photosynthesis, allocation, and respiration are represented in NPP predictions (Fig. 11.1a). While a soil respiration term is included in PnET-II (Kicklighter et al., 1994), the model does not explicitly simulate biomass accumulation or belowground C and N cycling. In contrast, TEM 4.0 (Raich et al., 1991; McGuire et al., 1992, 1993; Melillo et al., 1993) simulates interactions between and among above- and below-ground lumped C and N pools, using these transfers in its predictions of NPP (Fig. 11.1b). Because PnET-II emphasizes aboveground processes while TEM 4.0 represents both above- and belowground processes, the two models represent N limitations to growth in different ways. PnET-II requires foliar %N as an input, and assumes that foliar %N represents the constant N constraints experienced by the forest. TEM 4.0 simulates soil N cycling and N uptake, and assumes the vegetation experiences dynamic N constraints.

A second major question to be asked in this study is: How does the representation of CO_2 effects on C fixation affect model predictions of NPP under enhanced CO_2 and climate change? Field research has

suggested that increases in WUE are likely under enhanced CO_2 (for example, see Hollinger, 1987). Increased WUE would cause higher NPP in those biomes that experience water stress. However, a WUE increase can be caused by increased C assimilation, decreased stomatal conductance, or both (Eamus, 1991; Field et al., 1995; Bazzaz et al., 1996). If conductance decreases while C assimilation increases, WUE will increase even further. Thus WUE is a lumped measure of the end result of CO_2 increase. In PnET-II, CO_2 doubling is modeled as doubled WUE; thus PnET-II assumes that increases in C assimilation and decreases in conductance will sum to a 100% increase in WUE. In TEM 4.0, ambient CO_2 controls internal leaf CO_2, which drives C assimilation (McGuire et al., 1997). In this way, TEM 4.0 includes a physiologically based mechanism for predicting the impacts of enhanced ambient CO_2 on C assimilation.

Input Data Set Descriptions

For regional extrapolation, both PnET-II and TEM 4.0 require spatially explicit data sets of vegetation type and climate: monthly temperatures (maximum and minimum for PnET-II, average for TEM 4.0), monthly total precipitation, and monthly mean of total daily solar radiation. In addition, TEM 4.0 also requires a spatially explicit data set of soil texture. Although the models have similar input requirements, they have used different input data sets and different vegetation classification schemes to develop regional estimates. To minimize this source of variation in NPP estimates (cf. Pan et al., 1996) between the two models, we developed a common database and adapted our parameterizations to a common vegetation classification scheme.

For this study, we represented the forests of the northeastern U.S. with 115 pixels having a spatial resolution of 0.5° latitude × 0.5° longitude (see color plate Fig. 11.2). In previous analyses (Jenkins et al., 1999), we found little difference in regional NPP estimates made by these models at the 0.5° vs. the 60″ spatial resolution. The coarser spatial resolution greatly shortens the computational time required for analysis. Below, we describe how the input data sets were standardized for this study.

Land Cover Data Set

To describe the distribution of forest types in the northeastern U.S. (see Fig. 11.2), we aggregated a 30″ (roughly 1 km) data set developed from Advanced Very High Resolution Radiometer (AVHRR) data by Lathrop and Bognar (1994) to a 0.5° resolution as described by Jenkins et al. (1999). No attempt was made in the current analysis to take into account land that is not presently forested. PnET-II NPP estimates were created using parameter values for northeastern hardwood, pine, and spruce–fir

forests as described by Aber et al. (1995) and Ollinger et al. (1998). To adapt the TEM 4.0 parameterizations (McGuire et al., 1992) to this vegetation classification scheme, we parameterized (1) hardwoods as temperate deciduous forests, (2) pines as temperate coniferous forests, and (3) spruce–fir as boreal forests.

For both models, hardwood/spruce–fir pixels were run assuming each pixel consisted of 40% hardwood and 60% spruce–fir, and hardwood/pine pixels were run assuming each pixel consisted of 60% hardwood and 40% pine. These forest composition estimates were generated by comparing the original AVHRR-generated vegetation map with United States Department of Argiculture (USDA) Forest Service Inventory and Analysis data (Beltz et al., 1992). For pixels containing a mosaic of hardwood/spruce–fir forests or hardwood/pine forests, TEM 4.0 estimated NPP by weighting estimates made with each of the appropriate nonmosaic calibrations (cf. McGuire et al., 1995) with the percentage cover just described for these mosaic grid cells. Similarly, PnET-II predictions for mixed pixels were created by weighting estimates made using the pine, hardwood, or spruce–fir parameterizations with the percentage cover described above for each forest type.

Soils

Both PnET-II and TEM 4.0 use the concept of soil WHC (defined as field capacity minus wilting point) to represent the maximum amount of water that can be stored in the soil and made available to plants. But while PnET-II requires soil WHC as an input variable, TEM 4.0 uses soil depth and soil texture (as %[silt + clay]) to derive total volumetric soil water at field capacity, and then uses rooting depth to predict soil WHC. Soil WHC is used as an internal variable during TEM 4.0 simulations. A constant value of 12 cm has been used for soil WHC in all northeastern U.S. PnET analyses to date (Aber and Federer, 1992; Aber et al., 1995, 1997; Ollinger et al., 1998; Jenkins et al., 1999) and soil WHC was held constant at 12 cm for this study as well. To create equivalent NPP predictions using both models, we constrained the soil WHC used internally by TEM 4.0 to 12 cm.

Climate Input Data Sets

To examine the effect of climate change on NPP, we developed common data sets for both contemporary climate and future climate, as projected from five General Circulation Model (GCM) experiments.

Contemporary Climate

For all contemporary climate data, we selected the 115 pixels that represent this part of the northeastern U.S. from the Vegetation/

Ecosystem Modeling and Analysis Project (VEMAP) (Kittel et al., 1995). To develop these contemporary climate data, minimum and maximum monthly temperatures from weather stations were adiabatically adjusted to sea level using algorithms of Marks and Dozier (1992), georeferenced to the 0.5° grid, then readjusted to grid elevations. For TEM 4.0, mean monthly temperatures were determined by averaging the maximum and minimum temperatures for each month. Mean monthly precipitation was aggregated to the 0.5° resolution from a 10-km resolution data set developed using the PRISM model (Daly et al., 1994). CLIMSIM (a simplified version of MT-CLIM for flat surfaces (Running et al., 1987; Glassy and Running, 1994) was used to estimate daily solar radiation received at the canopy level, and these daily data were averaged to obtain the monthly means.

Climate Change Scenarios

Equilibrium climate change scenarios from five GCM experiments were used to create the forest NPP predictions presented here. Three of these five were also used to create continental-scale predictions during the VEMAP exercise (VEMAP Members, 1995). These are from the Geophysical Fluid Dynamics Laboratory (GFDL) (Wetherald and Manabe, 1988; Manabe et al., 1990; Wetherald et al., 1990), Oregon State University (OSU) (Schlesinger and Zhao, 1989), and the United Kingdom Meteorological Office (UKMO) (Wilson and Mitchell, 1987).

The other two GCM scenarios come from the Hadley Centre (Mitchell et al., 1995). The first includes only the radiative forcing due to greenhouse gases (the "Hadley/gas" scenario), and the second takes into account both the warming effects of greenhouse gases and the direct radiative effect of sulphate aerosols (the "Hadley/sulphate" scenario). Thus only one set of climate data in this experiment includes the effects of sulphate aerosols, which can influence climate directly by scattering and absorbing radiation, or indirectly by modifying the optical properties of clouds (Schimel et al., 1996a). In the short term, sulphate aerosols are likely to mitigate the warming influence of greenhouse gases (Mitchell et al., 1995), though considerable uncertainty exists about the spatial distributions of sulphate and other aerosols and about their individual and combined impacts on radiative forcing of climate change (Schimel et al., 1996a).

To find monthly minimum and maximum temperature projections for use in PnET-II, the difference between the GCM and VEMAP monthly mean temperatures was found for each of the 115 pixels. This difference was then added to the VEMAP monthly minima and maxima to create an estimate of the monthly minimum and maximum temperature under climate change for each pixel. This method assumes no change in the diurnal temperature range.

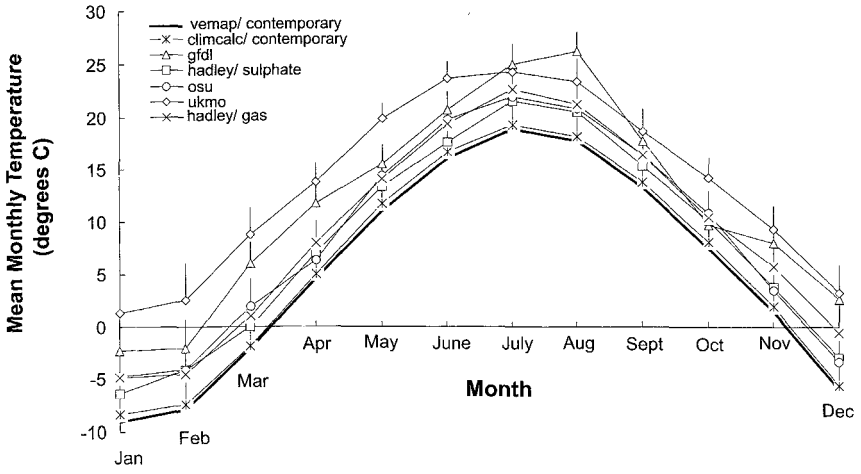


Figure 11.3. Comparison of GCM monthly mean temperature predictions for the northeastern region. Each point represents the average of 115 0.5° pixels, ±1 SD.

For the northeastern region, all of the GCM scenarios predict substantially warmer temperatures year-round. The UKMO and GFDL scenarios predict the warmest conditions under climate change, with regional yearly average temperature increases of 8.1 and 6.1°C, respectively. The Hadley/gas, OSU, and Hadley/sulphate scenarios predict smaller temperature increases, with regional yearly average increases of 3.6, 3.2, and 2.5°C, respectively (Fig. 11.3). Temperature projections made by the Climcalc model, a statistical model of contemporary climate based on latitude, longitude, and elevation, and created from weather station data collected in the region (Ollinger et al., 1995), are also plotted on Fig. 11.3 for comparison. The Climcalc and VEMAP predictions of contemporary monthly mean temperature agree closely; this agreement contrasts with the GCM projections, which differ more substantially from one another.

The difference between the VEMAP and Climcalc estimates of contemporary precipitation is greater than the corresponding difference between the contemporary temperature data sets. This difference is still small, however, compared with the projected changes in precipitation represented by the various GCM data sets (Fig. 11.4). Averaged regionally, the GCM scenarios all predict an increase in total annual precipitation for the northeastern region: +23.4% for UKMO; +19.0% for Hadley/sulphate; +18.5% for GFDL; +18.4% for Hadley/gas; and +10.9% for OSU. The GFDL scenario predicts the greatest seasonal variation in precipitation with 60 mm of precipitation occurring in August and 174 mm occurring in October.

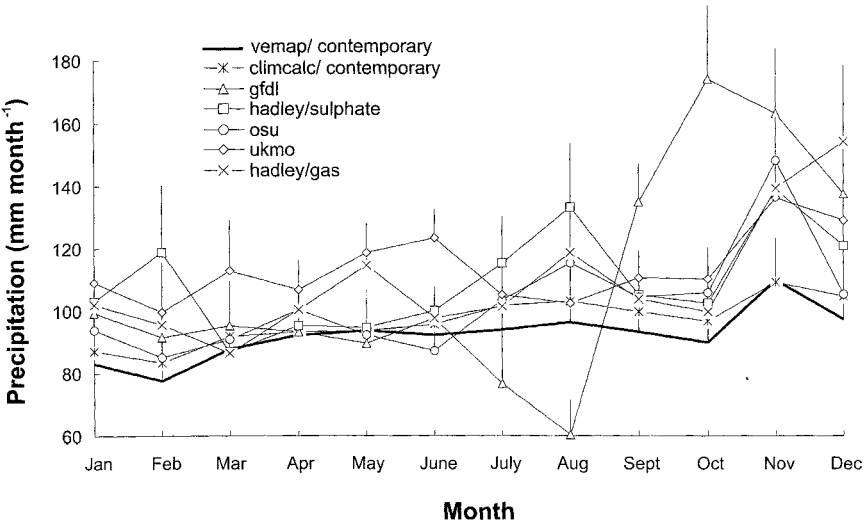


Figure 11.4. Comparison of GCM monthly precipitation predictions for the northeastern region. Each point represents the average of 115 0.5° pixels, ±1 SD.

The GCMs predict slight changes in solar radiation in the northeastern region (Fig. 11.5). During the winter, the two Hadley scenarios predict somewhat lower solar radiation than the other GCM scenarios, and the

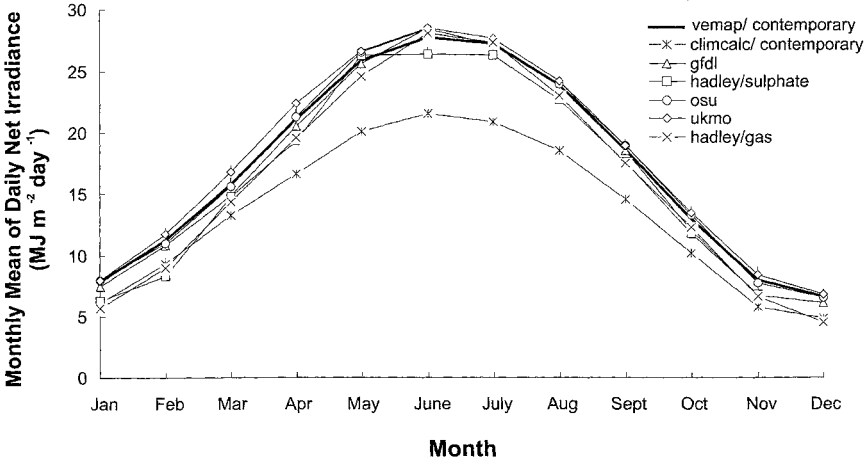


Figure 11.5. Comparison of GCM solar radiation predictions for the northeastern region. Both models use monthly mean of daily net irradiance as input. Each point represents the average of values for 115 0.5° pixels, ±1 SD.

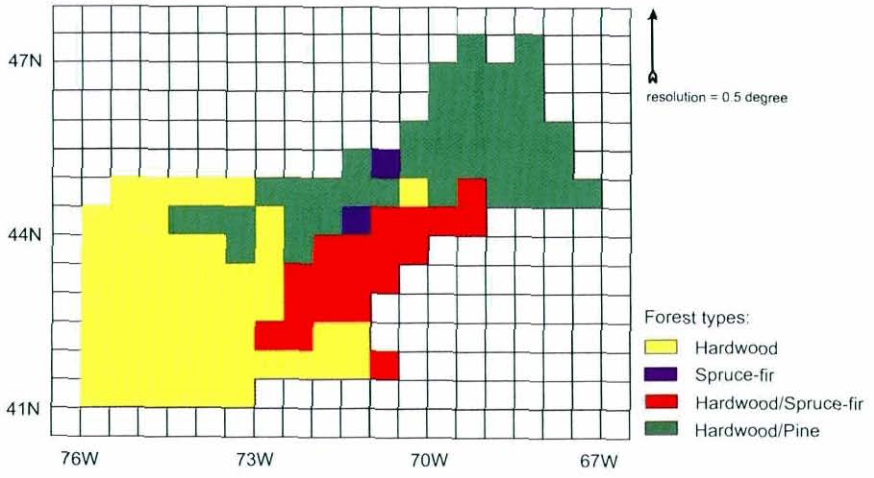


Figure 11.2. Forest classification for the portion of the northeastern region treated in this analysis. See text for details.

sulphate correction also moderately reduces the amount of radiation received during the growing season. The difference between the Climcalc and VEMAP representations of contemporary climate is larger than the differences between the predictions made by the GCM scenarios. Considerable uncertainty exists about the accuracy of the VEMAP solar radiation data at the continental and regional scales (Pan et al., 1996; Jenkins et al., 1999). Because ecosystem process models can be quite sensitive to solar radiation inputs, future research should be directed at reducing this uncertainty.

General Circulation Model Uncertainty

The 0.5° latitude by 0.5° longitude GCM estimates used in this study were interpolated from original data sets with a resolution of 5° latitude by 5° longitude. GCM predictions are less reliable at the regional scale than at larger scales (Kattenberg et al., 1996) due to the parameterizations of physical processes, which are less accurate at smaller scales (Gates, 1985; Ghan, 1992). Areas dominated by land–ocean interactions are especially prone to GCM uncertainty (Cooter et al., 1993). While regional climate projections such as those used in this analysis are necessarily uncertain, the GCM projections do represent a range of possible climate responses to radiative forcing. Analysis and comparison of model predictions of forest NPP under several of these scenarios provides us with a range of possible forest responses for a future in which the trajectory of climate change is uncertain.

Effect of Climate Change on Forest Net Primary Productivity

Regional Predictions

At the regional scale, the NPP predictions of the two models differ by only 3% for contemporary climate and by 10% for the various future climate scenarios (Table 11.1). Both models also predicted an increase in forest NPP under all climate change scenarios (see Table 11.1), with PnET-II predicting an average increase of 37.9% over the VEMAP contemporary scenario, and TEM 4.0 predicting an average increase of 30.0%. For both models, the largest increases in NPP (+58.2% for PnET-II and +54.7% for TEM 4.0) occurred under the UKMO climate. However, different scenarios induced the smallest increase in NPP for the two models. Net primary productivity estimated by PnET only increased by 30.0% under the Hadley/sulphate scenario, whereas NPP estimated by TEM 4.0 increased by only 17.7% under the GFDL scenario. PnET-II and TEM 4.0 NPP predictions increased by 2.5 and 6.2% less, respectively, under the Hadley/sulphate scenario than under the Hadley/gas scenario. Thus,

Table 11.1. NPP Predictions Made by PnET-II and TEM 4.0 under Contemporary and Enhanced CO_2 Conditions

Model	GCM Scenario	Biome-specific Averages (gOM m^{-2} yr^{-1}) (% difference from control)				Regional Total (TgOM yr^{-1})
		Hardwood[a]	Spruce–Fir[b]	Hardwood/ Spruce–Fir[c]	Hardwood/Pine[d]	
PnET-II	*VEMAP (control)*	*1367.60*	*890.40*	*1050.80*	*1186.80*	*313.14*
	GFDL	1838.41 (+34.4%)	983.56 (+10.5%)	1283.76 (+22.2%)	1819.63 (+53.3%)	418.32 (+33.6%)
	Hacdley gas only	1870.31 (+36.8%)	917.46 (+ 3.0%)	1222.24 (+16.3%)	1781.10 (+50.1%)	414.99 (+32.5%)
	Hadley sulphate	1839.26 (+34.5%)	899.30 (+ 1.0%)	1202.12 (+14.4%)	1726.24 (+45.5%)	407.06 (+30.0%)
	OSU	1907.36 (+39.5%)	910.63 (+ 2.3%)	1245.20 (+18.5%)	1813.88 (+52.8%)	422.93 (+35.1%)
	UKMO	2199.67 (+60.8%)	1124.22 (+26.3%)	1443.85 (+37.4%)	2247.13 (+89.3%)	495.38 (+58.2%)
TEM 4.0	*VEMAP (control)*	*1540.07*	*583.55*	*895.48*	*1295.35*	*324.17*
	GFDL	1757.85 (+14.1%)	709.05 (+21.5%)	1093.51 (+22.1%)	1602.62 (+23.7%)	381.68 (+17.7%)
	Hadley gas only	1941.44 (+26.1%)	744.40 (+27.6%)	1151.34 (+28.6%)	1674.89 (+29.3%)	412.38 (+27.2%)
	Hadley sulphate	1844.17 (+19.7%)	707.40 (+21.2%)	1093.40 (+22.1%)	1603.13 (+23.8%)	392.28 (+21.0%)
	OSU	1983.64 (+28.8%)	745.55 (+27.8%)	1159.77 (+29.5%)	1683.34 (+30.0%)	418.72 (+29.2%)
	UKMO	2417.64 (+57.0%)	906.45 (+55.3%)	1368.05 (+52.8%)	1943.42 (+50.0%)	501.44 (+54.7%)

[a] $n = 54$ pixels for each scenario.
[b] $n = 2$ pixels for each scenario.
[c] $n = 40$ pixels for each scenario.
[d] $n = 19$ pixels for each scenario.

while sulphate aerosol correction does impact model predictions, larger differences exist between NPP predictions made using unrelated GCM scenarios. In this analysis at the regional scale, differences between the GCM climate input data sets were more important contributors to variability in model predictions than differences between the models.

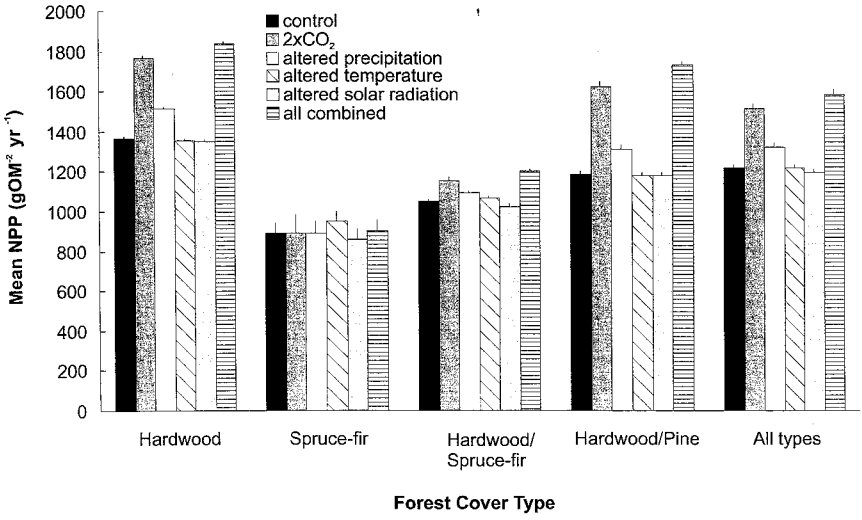
Biome-level Predictions

The biome-level differences evident in the NPP predictions for contemporary climate were emphasized when the GCM scenarios were used to drive the models. For all GCM scenarios, PnET-II predicted that NPP in the higher-productivity forests (hardwood and hardwood/pine) would increase more than in the lower-productivity forests (spruce–fir and hardwood/spruce–fir), while TEM 4.0 predicted that NPP would increase by roughly the same percentage for each biome (see Table 11.1).

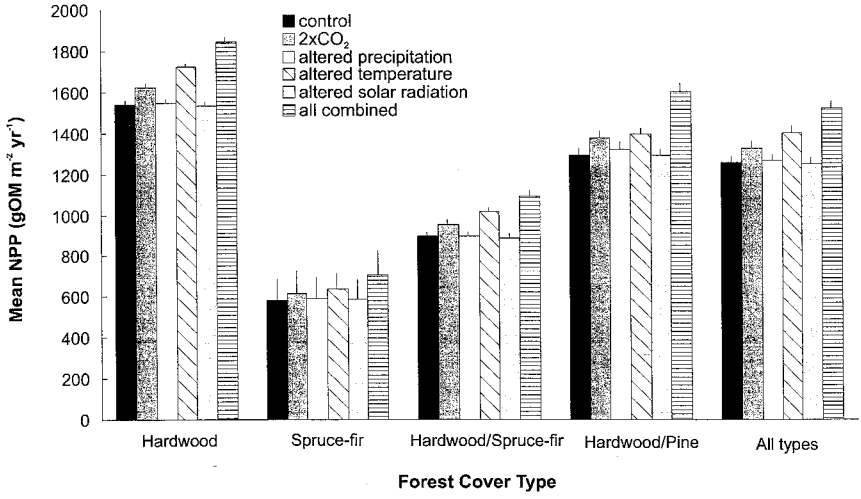
To understand better the reasons behind these differences, we performed a series of experiments with both models in which we used values of one variable (i.e., atmospheric CO_2 concentration, air temperature, precipitation, or solar radiation) from the Hadley/sulphate GCM scenario together with values for all other variables from the VEMAP contemporary climate scenario as inputs to the models. The Hadley/sulphate GCM scenario was used for this exercise because it takes into account the radiation-scattering effects of sulphate aerosols, which are likely to exert a significant effect on climate in the future (Mitchell et al., 1995; Schimel et al., 1996a). We then examined how the results of these sensitivity experiments (Fig. 11.6) are related to the different conceptualizations of forest ecosystem dynamics by the two models.

PnET-II

Because doubled CO_2 is parameterized as a doubling of WUE, the forest types that are most limited by water availability in PnET-II are expected to respond the most dramatically to CO_2 increase. A previous sensitivity analysis with PnET-II (Ollinger et al., 1998) suggested that water availability was the factor most limiting to hardwood forests under the range of conditions typical of the northeastern region. Consistent with the results from the previous analysis, in this study PnET-II predicted a dramatic increase in hardwood NPP when CO_2 doubling was added to contemporary climate (see Fig. 11.6a). The forest types with a hardwood component also experienced an increase in NPP due to CO_2 doubling. In addition, hardwood NPP responded positively to the precipitation increase from the VEMAP to the Hadley/sulphate scenarios (see Fig. 11.6a). The NPP change with increased precipitation was not as dramatic as the effect of doubled CO_2, because the 19.0% increase in precipitation did not alleviate as much water stress as did the doubled WUE.



(a)



(b)

Figure 11.6. Biome-level responses to individual climate variables from Hadley/sulphate GCM (a, PnET-II; b, TEM 4.0). Within each forest type, each bar represents the mean ±1 SD for one run with one Hadley/sulphate climate variable substituted for the equivalent VEMAP contemporary variable. "Altered" variables are from the Hadley/sulphate GCM; all others are from the VEMAP contemporary climate scenario, except for the "all combined" run, in which all of the Hadley/sulphate variables were applied at once.

For the range of conditions currently encountered by northeastern forests, PnET-II predicts that NPP in the spruce–fir biome is more limited by solar radiation and temperature than by water (Ollinger et al., 1998; Jenkins et al., 1999). Thus the 2.5°C average regional increase predicted by the Hadley/sulphate scenario caused a slight increase in predicted NPP for spruce–fir forests. Similarly, the absence of water limitation in spruce–fir forests means that spruce–fir NPP is more tightly linked to solar radiation and PAR availability. As a result, the decline in solar radiation predicted by the aerosol-corrected Hadley/sulphate scenario caused a slight decline in spruce–fir NPP (see Fig. 11.6a).

When all of the Hadley/sulphate climate variables were applied simultaneously with doubled CO_2, predicted NPP was higher in all forest types (except spruce–fir) than for any of the variables applied alone. The combined impacts of alleviated water stress and increased precipitation on hardwood NPP were important determinants of productivity in all biomes with a hardwood component (see Fig. 11.6a). However, the effects were not additive, suggesting that interactions between water and temperature may be key predictors of modeled NPP under climate change. Spruce–fir NPP under the Hadley/sulphate GCM climate combined with doubled CO_2 was approximately the same as that found under contemporary climate because the enhanced NPP caused by higher temperatures compensated for the diminished NPP caused by lower solar radiation.

TEM 4.0

In TEM 4.0, enhanced atmospheric CO_2 increases GPP in all biomes if sufficient light and N are available. TEM 4.0 does not prescribe a WUE value, but the model assumes that total canopy conductance and actual evapotranspiration do not change in response to elevated CO_2 so that the enhancement of GPP by CO_2 fertilization causes an effective increase in WUE (cf. Pan et al., 1998). Unlike PnET-II, which assumes a doubling of WUE with doubled CO_2, the effective WUE estimated by TEM increased by only 5 to 6% for all forest biomes in the northeastern U.S. with a doubling of atmospheric CO_2. The model estimates larger increases in effective WUE in warmer and drier biomes (cf. Pan et al., 1998). The precipitation increase from the VEMAP to the Hadley/sulphate scenario had little effect on the TEM 4.0 NPP predictions for the various biomes (see Fig. 11.6b), because TEM 4.0 predicts little or no water stress in the northeastern region under the VEMAP contemporary climate.

Using TEM 4.0, the temperature increase from the VEMAP to the Hadley/sulphate scenario caused a more pronounced NPP increase for all biomes than did the doubling of atmospheric CO_2 (see Fig. 11.6b). In addition to the direct effects of temperature on GPP, temperature increases also enhanced decomposition and N mineralization rates. Accelerated N mineralization increased N availability to vegetation,

resulting in higher NPP (Pan et al., 1998). This result is also consistent with the continental-scale results of Schimel et al. (1997), who found a tight correlation between N mineralization and NPP in TEM 4.0 predictions under contemporary climate.

When all of the Hadley/sulphate climate variables were applied simultaneously with doubled atmospheric CO_2, predicted NPP for all forest types was higher than for any of the climate variables applied alone (see Fig. 11.6b). Using TEM 4.0 under climate change and enhanced ambient CO_2, both the increase in N availability caused by increased temperature and the increase in C availability that occurs under enhanced atmospheric CO_2 allowed larger increases of NPP to occur than under either enhanced atmospheric CO_2 or enhanced temperatures alone.

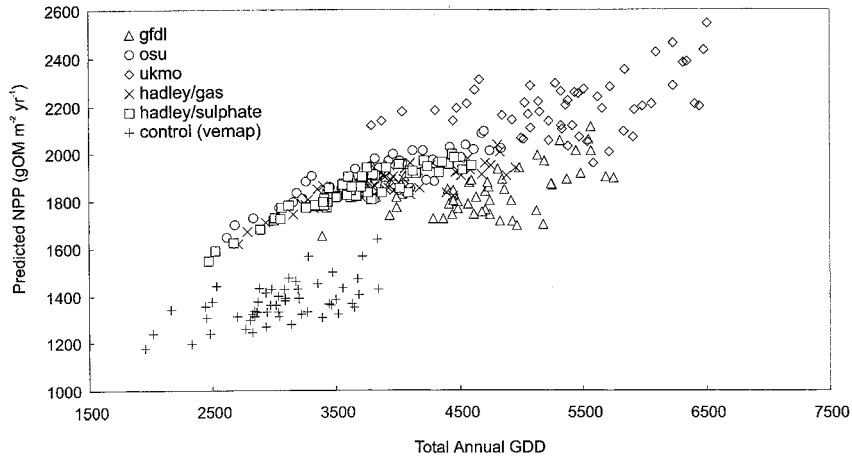
Effects of Climate Interactions on Net Primary Productivity

At this point in our analysis of forest NPP in the northeastern U.S. under climate change and enhanced CO_2, TEM 4.0 estimates appear to be primarily limited by temperature, while PnET-II estimates appear to be limited primarily by water. However, PnET-II and TEM 4.0 both estimated similar large increases in NPP associated with the large increases in temperature under the UKMO climate (see Table 11.1). In addition, the small increase in NPP estimated by TEM 4.0 under the GFDL scenario, which predicted drier summers, indicates that TEM 4.0 estimates of NPP are also sensitive to changes in precipitation. To explore this issue further, we expand our analysis to include results from model simulations using the wider range of climate variables in all five GCM scenarios.

Increased temperature can affect phenology as well as increasing photosynthesis. Myneni et al. (1997) have reported satellite evidence for a lengthening of the growing season in the northern latitudes between 1981 and 1991 as a potential result of climate change. Total annual growing degree days (GDD) is a useful measure of these combined effects and is calculated as the annual sum of temperatures for all days with average temperature greater than 0°C. Because our regional NPP estimates are based on monthly air temperature data, we can calculate GDD as:

$$GDD = \Sigma(\text{monthly average temperature}) \times (\text{days in month}) \quad (1)$$

for all months with average temperature greater than 0°C. A comparison of predicted NPP with annual GDD for both models and all GCM scenarios (Fig. 11.7) shows the extent to which each model appears to be temperature-driven, and the comparative relationship between GDD and NPP for the different GCM scenarios as predicted by each model. For the range of climate conditions predicted by the GCM scenarios used in this analysis, GDD was a good predictor of hardwood NPP for both PnET-II



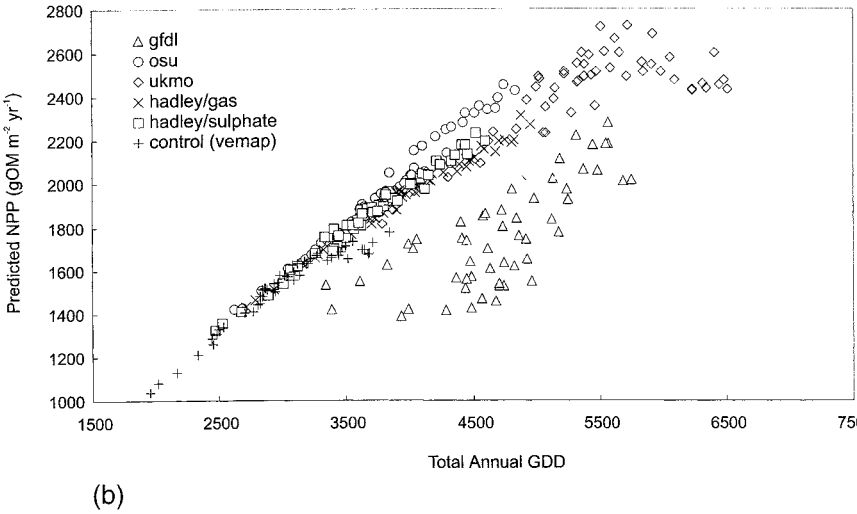


Figure 11.7. Predicted NPP vs. annual GDD for hardwood forest (a, PnET-II; b, TEM 4.0). Each point represents NPP as predicted for one pixel under one GCM scenario.

and TEM 4.0 (Table 11.2). The inclusion of six different scenarios representing both contemporary and changed climates widened the GDD range significantly for this analysis, resulting in strong correlations between GDD and predicted NPP. Annual precipitation and growing season precipitation were also good predictors of modeled NPP for both PnET-II and TEM 4.0 (see Table 11.2).

Table 11.2. R^2 Values from Linear Regression Analyses between Predicted NPP and Each of the GCM-predicted Climate Variables

Model	Forest Type	Average Yearly Temperature (°C)	GDD[a]	Net Irradiance ($J\ m^{-2}\ day^{-1}$)	Precipitation ($cm\ yr^{-1}$)	Growing Season Precipitation ($cm\ season^{-1}$)	Suitability[b]
PnET-II	Hardwood	0.65	0.62	0.03	0.42	0.21	0.70
	Spruce–fir	0.66	0.62	0.43	0.04	0.17	0.68
	Hardwood/ spruce–fir	0.72	0.68	0.15	0.42	0.25	0.74
	Hardwood/pine	0.74	0.72	0.05	0.64	0.23	0.73
	All types	0.61	0.58	0.04	0.25	0.13	0.59
TEM 4.0	Hardwood	0.69	0.68	0.01	0.28	0.26	0.83
	Spruce–fir	0.70	0.70	0.26	0.30	0.45	0.88
	Hardwood/ spruce–fir	0.61	0.57	0.03	0.29	0.28	0.68
	Hardwood/pine	0.78	0.73	0.01	0.61	0.30	0.80
	All types	0.58	0.56	0.02	0.17	0.19	0.63

[a] Defined as the yearly sum of (monthly average temperature × days in month) for all months with average temperature >0°C.
[b] Defined as ((Growing season precipitation × GDD)/10,000).

When predicted NPP was plotted against GDD for both models (see Fig. 11.7), predictions made using the GFDL scenario were noticeably lower than predictions made using any of the other GCM scenarios. Growing season precipitation under the GFDL scenario was clearly lower than that of the other GCM scenarios (Fig. 11.4); for both models, it appeared that water stress was severely limiting productivity under this scenario. This suggests that the NPP predictions of both models under future climates may be influenced by both water availability and temperature.

To examine the interactions between growing season precipitation and GDD, we developed a diagnostic index of temperature and water suitability, defined as:

$$\text{"suitability"} = (\text{growing season precipitation} \times \text{total annual GDD})/10,000 \quad (2)$$

where growing season precipitation (cm season^{-1}) is the precipitation that occurs between May 1 and October 1. At high values of the suitability index, water and temperature are not limiting, whereas NPP is limited by water availability, temperature, or a combination of these factors at low suitability values (Fig. 11.8). Linear regression analyses indicated that this index of the interaction between precipitation and temperature was a better predictor of variability in model NPP under climate change and enhanced CO_2 than any of the climate variables alone, for all forest types and both models (see Table 11.2). The predictive power of the suitability index suggests that simultaneous accurate predictions of both temperature and precipitation are critical for NPP predictions under a changed climate.

Carbon Dioxide Fertilization and Water Use Efficiency

The stepwise increase in PnET-II hardwood NPP predictions from the VEMAP 1×CO_2 climate to the GCM 2×CO_2 scenarios (see Figs. 11.7a, 11.8a) resulted from the doubling of WUE to estimate the effects of doubled CO_2 on NPP. This approach contrasts with the approach of TEM 4.0, which causes a more continuous NPP increase from contemporary to future climate scenarios (see Figs. 11.7b, 11.8b). In experiments under doubled atmospheric CO_2, WUE increases have ranged widely though the increases are usually less than 100% (Eamus and Jarvis, 1989; Eamus, 1991). Thus, doubling WUE may overestimate the influence of doubled atmospheric CO_2 on NPP. In addition, seasonal conditions and temperature may influence the degree of CO_2 enhancement of WUE, and different patterns of C gain (and WUE increase) may be experienced by different parts of individual plants (Eamus, 1991; Bazzaz et al., 1996). The availability of nutrients such as N may also limit the benefits of CO_2 fertilization (McGuire et al.,1997; Pan et al., 1998; Kicklighter et al., 1999). These considerations potentially argue in favor of a more dynamic,

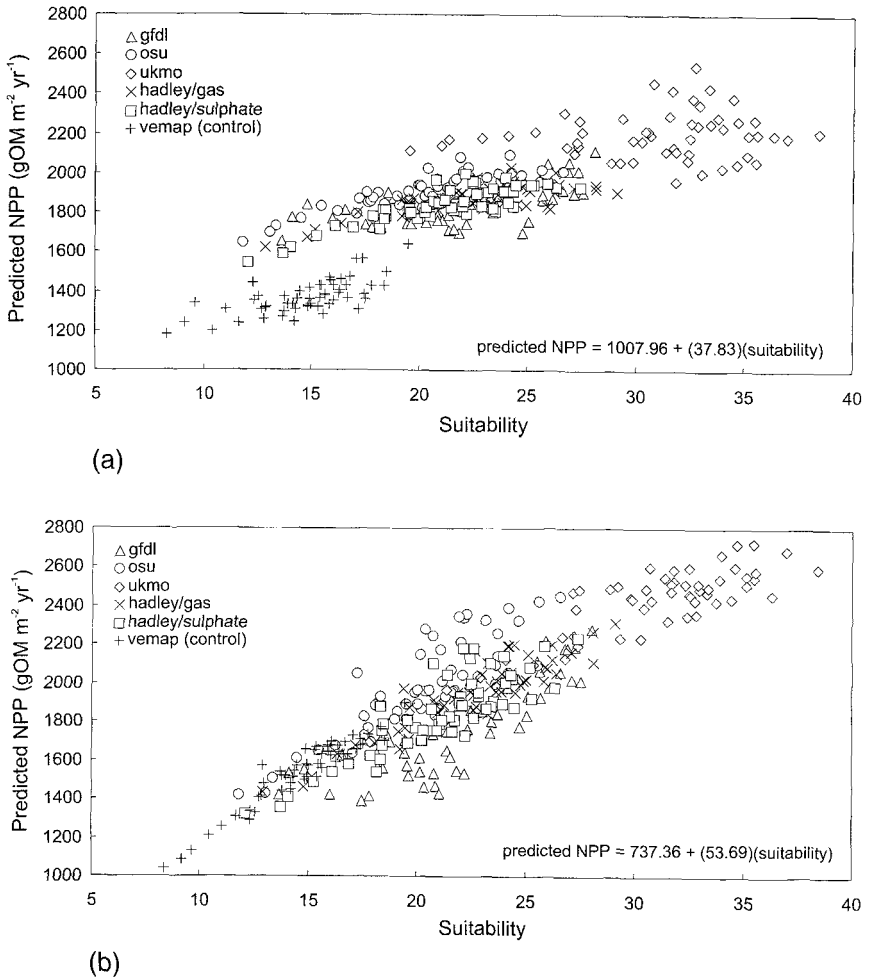


Figure 11.8. Predicted NPP vs. suitability index for hardwood forest (a, PnET-II; b, TEM 4.0). Each point represents NPP as predicted for one pixel under one GCM scenario. The best-fit linear regression equations are shown for each model (see Table 11.2 for R^2 values).

physiologically based parameterization of GPP response to enhanced CO_2, such as that found in TEM 4.0. However, the focus on GPP response to the exclusion of a stomatal response might underestimate the direct effects of enhanced CO_2 on C gain. In the absence of decisive and quantitative information about patterns of change in WUE and C assimilation under increased CO_2, doubling WUE and the more physiologically based approaches may be equally accurate.

Influence of Belowground Processes on Predicted Net Primary Productivity

Both the NPP predictions and the relative strengths of the water, temperature, and solar insolation limitations on NPP were similar for PnET-II and TEM 4.0 in this analysis despite their very different representations of the process-based limitations on NPP (see Tables 11.1 and 11.2). Specifically, TEM 4.0 includes belowground N availability in its NPP predictions by including decomposition and N mineralization routines, which are driven by climate variables, while PnET-II includes belowground N availability in its predictions via foliar %N, which is determined by forest type and remains constant. While it might be argued that including all belowground feedbacks between climate and nutrient availability offers the potential for a more accurate representation of forest ecosystem processes, there is evidence for steady-state correlations between water and nutrient limitations on NPP (Aber et al., 1991; Schimel et al., 1996b). If a model gives an accurate reflection of nutrient limitations at equilibrium (e.g., by correlating photosynthetic rate with foliar %N), then algorithms representing detailed soil processes may be extraneous. The limitation of such a model is that it does not represent conditions other than those occurring at steady state. Under transient conditions, representation of detailed belowground processes will be more important because the water, N, and C budgets are likely to respond to perturbation on different time scales (Schimel et al., 1996b), and NPP predictions will vary accordingly.

Other Issues

These two models, with their different structures and parameterization approaches, made similar predictions of forest NPP under changed climate scenarios. However, other factors likely to influence forest productivity in the northeastern U.S. were not considered here. For example, changing temperature and precipitation regimes during the period before equilibrium conditions are reached (transient conditions) are likely to cause forest NPP patterns different from those expected under equilibrium conditions (Pastor and Post, 1988, 1993; Smith and Shugart, 1993; Melillo et al., 1996). Other anthropogenically induced stresses, such as N deposition, are common in the region and may impact nutrient cycling and production rates in the future (Aber et al., 1989; Ollinger et al., 1993; Magill et al., 1996; Townsend et al., 1996; Vitousek et al., 1997; Nadelhoffer et al., 1999). Finally, past forest clearing and agriculture may have a lasting impact on current and future nutrient cycling and forest production (Cronon, 1983; Aber and Driscoll, 1997; Aber et al., 1997; Magill et al., 1997; Compton et al., 1998). Model analyses have not yet perfected techniques to predict forest NPP under each of these

conditions, but progress is being made. In this section, we present some examples of our work in this area.

Transient Analyses

The variability inherent in field-measured climate data contributes substantially to variability in NPP predictions (Aber and Driscoll, 1997). Unlike field-measured climate data, GCM equilibrium scenarios capture only the long-term changes in climate that might be expected as a result of greenhouse-gas forcing. To examine the effects of climate variability on model NPP predictions, we used transient climate data spanning 1950 to 1995 as input to transient versions of both PnET-II and TEM (TEM 4.1, see Tian et al., 1999).

Climate Data Sets

The transient temperature and precipitation data were developed from the temperature anomalies of Jones et al. (1991) and the precipitation anomalies of Hulme (1995) as described by Tian et al. (1999). For the two 0.5° cells containing the Harvard Forest (HF) in north central Massachusetts and the Hubbard Brook Experimental Forest (HBEF) in central New Hampshire, the gridded data appear to damp out some of the year-to-year temperature variability and to overestimate slightly the mean annual temperature (Fig. 11.9). The gridded precipitation data capture accurately the trends in year-to-year variability of total annual precipitation (Fig. 11.10). However, the site-to-site variability in precipitation is diminished by the gridded precipitation data. For example, the drought in the mid-1960s was extremely severe at HF (see Fig. 11.10a) and less severe at HBEF (see Fig. 11.10b). The gridded data underpredict the drought's severity at HF and overpredict drought severity at HBEF, apparently smoothing drought effects across the region.

Model Comparisons

We used the gridded transient data presented in Figs. 11.9 and 11.10 to predict NPP and NEP using PnET-II and TEM 4.1 for the HF and HBEF sites. For PnET-II, foliar %N values of 2.0 and 2.4% were used in these predictions for both sites, because these foliar %N values represent the likely range of hardwood foliar %N values for the northeastern region as a result of site quality and previous land use history. The 2.4% value was measured at HBEF by Whittaker et al. (1974). The 2.0% value represents the average of two measured values in different areas of the Harvard Forest: 1.8% in the control hardwood stand used in the chronic N experiment, as measured by Aber et al. (1993b); and 2.2% in the area around the eddy correlation tower, as measured by M.E. Martin and J.D. Aber. While there is little direct evidence for reduced foliar %N in

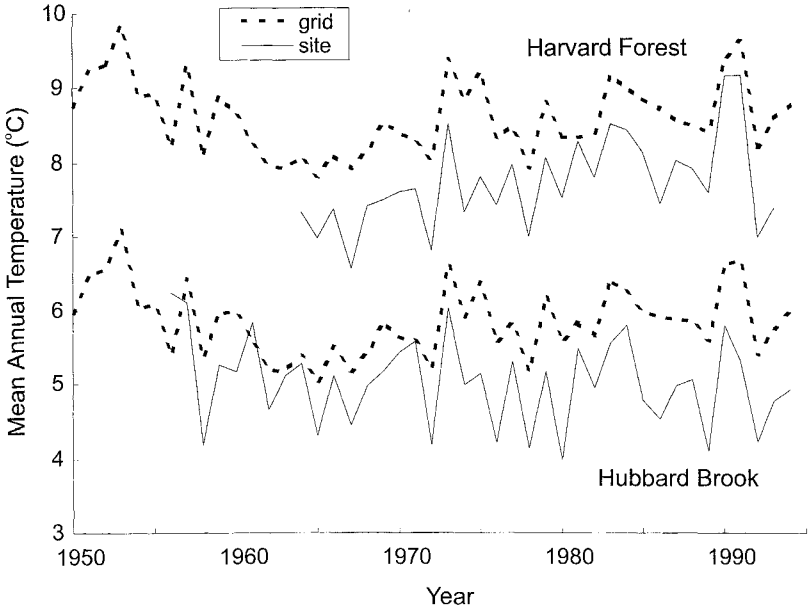


Figure 11.9. Comparison of site-measured transient temperature data and gridded temperature data for Harvard Forest and Hubbard Brook.

severely disturbed sites, there is convincing evidence for increased N uptake and foliar %N in N-rich sites (cf. Magill et al., 1997). Low soil N availability as a result of low site quality or past disturbance is likely to result in lower foliar %N on these sites, compared with undisturbed or high quality sites.

Perhaps the most obvious result from the model predictions made using transient climate data is that interannual climate variability contributes substantially to interannual variability in predicted NPP (Fig. 11.11). With PnET-II, however, the range expected as a result of climate variability was similar to or smaller than the range expected as a result of differences in foliar %N. This result is consistent with the findings of Goodale et al. (1998), who reported that PnET-predicted NPP in Ireland was more sensitive to differences in foliar %N (representing site quality and past land use history) than to climate change.

The absence of clear trends with time in this analysis suggests that more than four decades of measured data will be required in order to discern climate trends from transient data or to identify NPP and NEP trends from model predictions using the transient climate data. As suggested by Aber and Driscoll (1997), the variable characteristics of field-measured time series data should be represented in data sets representing future transient conditions.

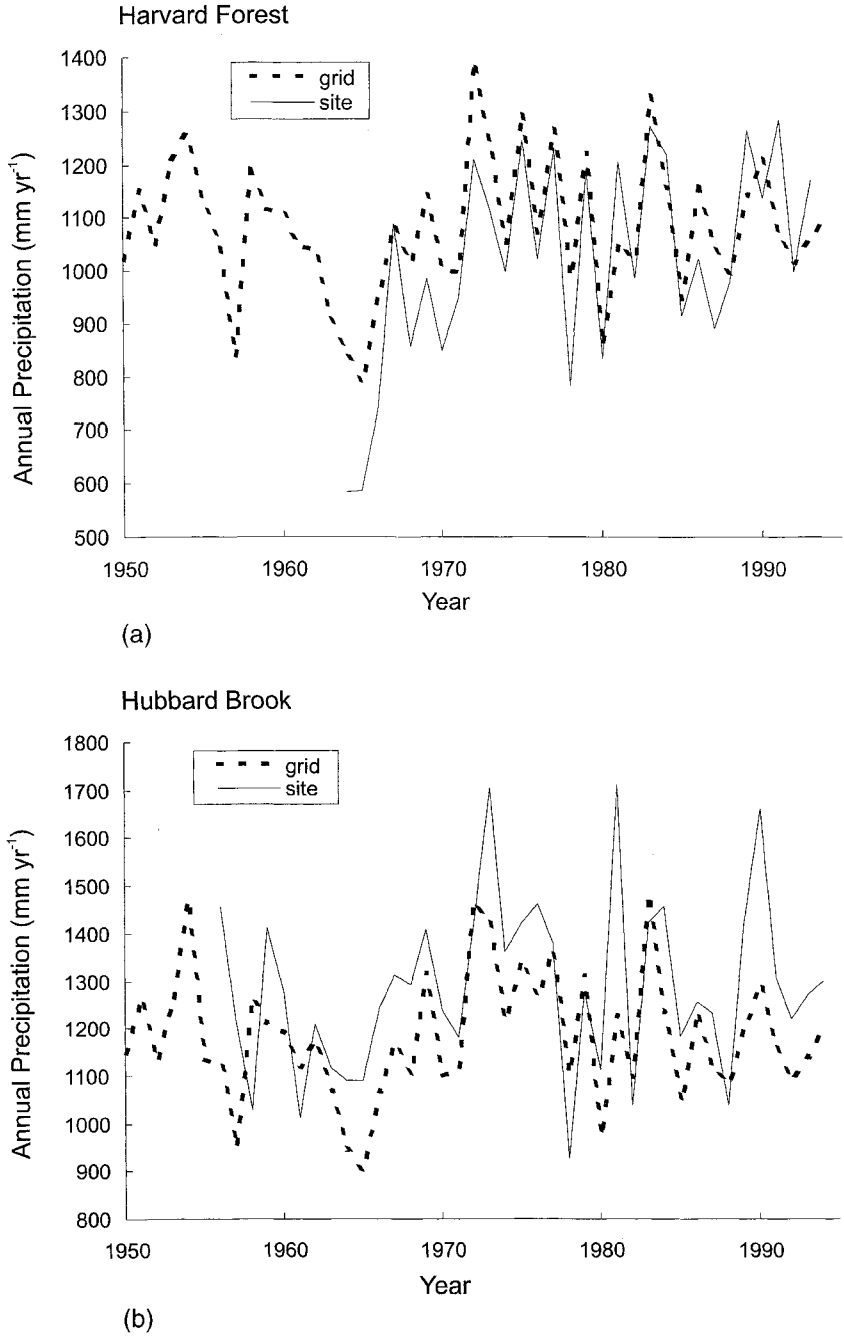


Figure 11.10. Comparison of site-measured transient precipitation data and gridded precipitation data for (a) Harvard Forest and (b) Hubbard Brook.

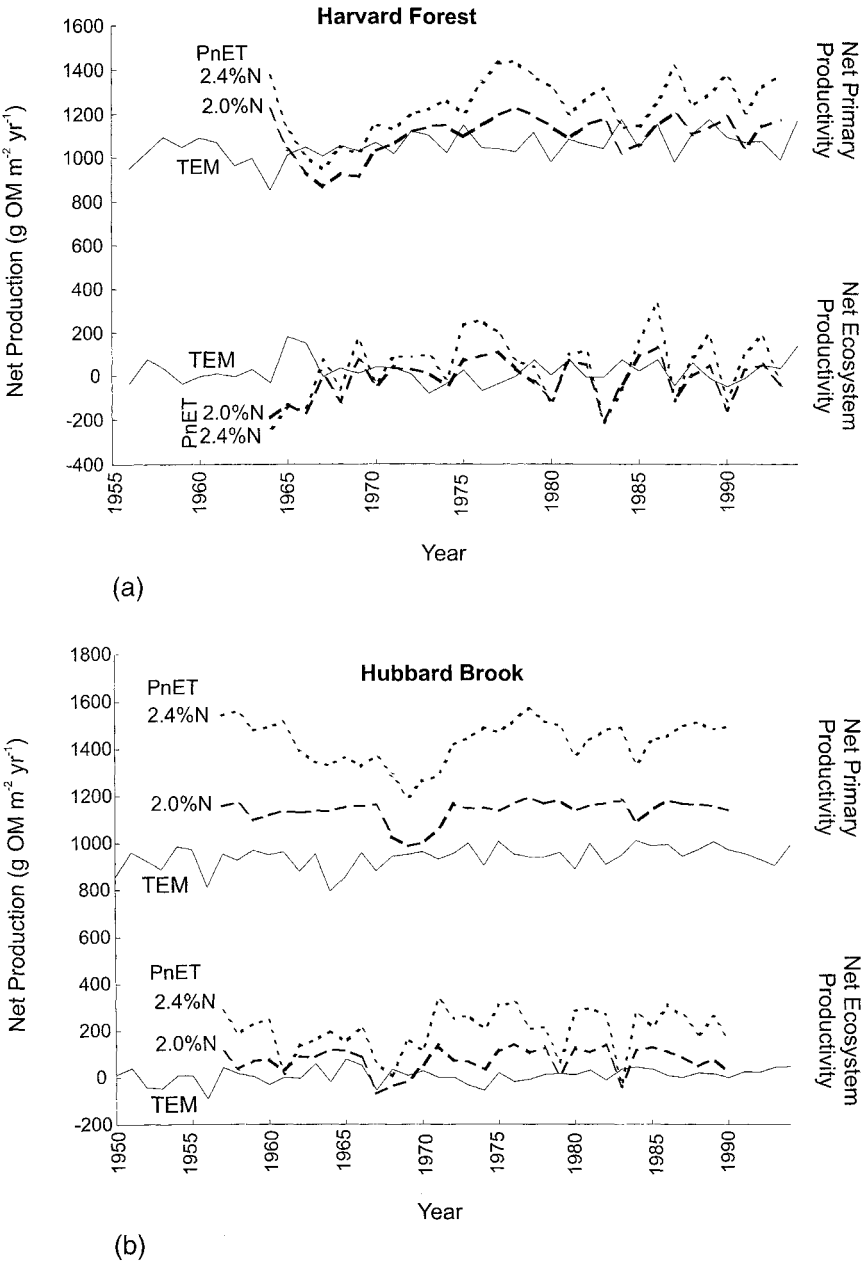


Figure 11.11. Transient predictions of NPP and NEP made by PnET-II and TEM 4.1 for (a) Harvard Forest and (b) Hubbard Brook.

At the HF site, the NPP and NEP estimates made by PnET-II (using the 2.0% foliar N value most appropriate for that site) and TEM 4.1 agreed closely (see Fig. 11.11a). When the models were applied to the HBEF site, on the other hand, the TEM 4.1 NPP predictions were lower on average, while PnET-II predictions (using the 2.4% foliar N most appropriate for that site) were higher (see Fig. 11.11b). These results reflect the model biases described earlier in the chapter.

TEM does not predict water stress for the northeastern region. As a result, temperature is most likely to be the driving variable for TEM predictions in this region under contemporary conditions. The warmer temperatures at HF, as compared with those at HBEF (see Fig. 11.9) caused TEM to predict higher NPP at HF than HBEF (see Fig. 11.11). On the other hand, PnET-II does predict water stress at HF (Aber et al., 1995). The increased precipitation at HBEF (see Fig. 11.10) reduced water stress at that site and caused PnET-II to predict higher NPP despite the cooler temperatures (see Fig. 11.11b). The cooler temperatures at HBEF also caused lower respiration rates, further contributing to the higher predicted NPP at HBEF than at HF.

Nitrogen Deposition and Land Use

Land use history and atmospheric deposition are two additional important change agents in the northeastern U.S. Interactive effects of these two can be important as land use, especially for forest harvesting or agriculture, can result in long-term reductions in N cycling in forested or reforested sites (Aber and Driscoll, 1997), which may be partially offset by increased N deposition. Nitrogen cycling rates are clearly linked with forest NPP (Pastor et al., 1984; Reich et al., 1997), suggesting that additions or extractions of N will impact C cycling rates as well.

To simulate the effects of N deposition and land use history on forest NPP at several sites in the northeast, we used PnET-CN, a model built upon PnET-II but which includes biomass storage terms for wood, roots, and soil organic matter, and which adds N pools and cycling to all compartments (Aber et al., 1997). Of critical importance for this analysis, PnET-CN does not assume a constant N availability to vegetation (via the foliar %N parameter). Rather, foliar N concentrations are predicted by the model and may change year-to-year depending on the relative availability of C and N to plants. PnET-CN also adds a "Scenario" subroutine, called at the beginning of each simulated month, which allows for the input of information on biomass removal, N deposition, and other variables such as climate change or experimental manipulations. The model has performed well when measured against streamflow and dissolved inorganic N (DIN) data at diverse sites around the northeastern U.S. (Aber and Driscoll, 1997; Aber et al., 1997), and

suggests that land use events can have very long-lasting (2–3 centuries) effects on N cycling.

Several forested sites within the White Mountains of New Hampshire having contrasting land use histories were used to examine the relative effects of N deposition and land use change on predicted NPP. These include (1) the Bowl Natural Area (BNA), one of the last remaining mixed deciduous and coniferous forests in the northeastern U.S. with no history of logging, human settlement, or forest fire (Leak 1974); (2) Cone Pond, a 53-ha catchment dominated by mixed coniferous vegetation (80%), with a smaller amount of northern hardwood cover (15%) which was severely burned in 1820 and has been relatively undisturbed since (Bailey et al., 1995, 1996); (3) Watershed 6 (W6), the reference watershed at HBEF, which was logged intensively from 1910 to 1917 and experienced some salvage removals after the hurricane of 1938; (4) Watershed 4 (W4), which was commercially clearcut in the early 1970s in 25-m wide strips along elevational contours, with every third strip cut every second year over 6 years; (5) Watershed 5 (W5), which was whole-tree harvested in 1983 to 84; and (6) Watershed 2 (W2) which was experimentally devegetated for three years beginning in 1965 (see Bormann and Likens [1979] for a description of the HBEF site and the experimental manipulations performed there).

Mean atmospheric deposition of DIN (nitrate-N [NO_3^--N] plus ammonium-N [NH_4^+-N]) has been estimated at 0.87 g N m^{-2} yr^{-1} for the HBEF, representing bulk wet deposition of 0.69 g N m^{-2} yr^{-1} for the period 1964 to 1991 (Butler and Likens, 1991; Likens, 1992; Likens and Bormann, 1995) and dry deposition of 0.18 g N m^{-2} yr^{-1} for the year 1989. For the simulations that included the effects of atmospheric inputs (ambient N deposition), N deposition was assumed to have increased linearly from 25% of these values to the current values beginning in 1900. Runs without N deposition effects (background N deposition) assume a constant rate of N deposition equal to 25% of current ambient values. Monthly climate data from the existing long-term records at the HBEF were used as input to the model for all sites, as described by Aber and Driscoll (1997).

Changes in NPP over time are compared for the two most extreme land use cases (BNA and W2) in Fig. 11.12. The BNA, with no prior history of N removals, showed slightly higher NPP values than W2 before the devegetation experiment, and a minor increase in NPP with ambient N deposition included. During devegetation, and for 10 years following, N availability was not limiting in W2, first due to reduced plant demand during the period of reestablishment, and then due to increased N availability because of the effects of disturbance on soil C/N ratios. During this 10-year disturbance and reestablishment period, N deposition had no effect on NPP at W2. After 1980, the long-term effects of N removals caused NPP to be more severely N-limited at W2 than BNA, with lower

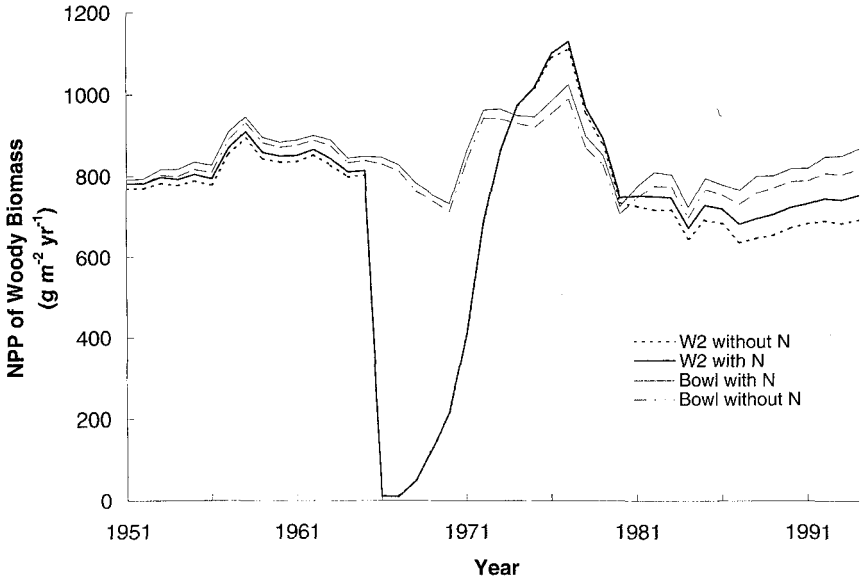


Figure 11.12. Transient PnET-CN predictions of woody NPP for two sites with different land use histories, showing the effect of N deposition on predicted NPP.

rates of NPP at W2. These results are consistent with those of Aber et al. (1997), who found from analyses using PnET-CN that while N cycling and NPP might pulse soon after disturbance, the long-term legacy of biomass and N removal is a reduction in N cycling rates. Ambient N deposition can reverse this trend, but only very slowly.

Fig. 11.13 expresses the change in NPP for each year caused by ambient vs. background N deposition for all sites. In general, increased N deposition caused small increases in NPP at all sites, with these increases due to N deposition accelerating slightly with time. Differences between sites due to disturbance histories were minor except during periods of vegetation reestablishment (e.g., W2 1966 to 1975 and W5 1984 to 1989). During these reestablishment periods, forest production was not N-limited so N deposition had no effect on predicted NPP.

The scale of current NPP differences due to contrasting land use histories is so small as to be undetectable using currently available field methods. Similarly, interannual variation in both absolute NPP values and differences between NPP predictions made using ambient and background N deposition scenarios is so high that neither could be detected by field measurement. Transient model analyses, however, can predict forward in time by decades or centuries to estimate the long-term legacies of land use history and atmospheric deposition. The transient modelling approach is especially useful for cases such as this one, in which

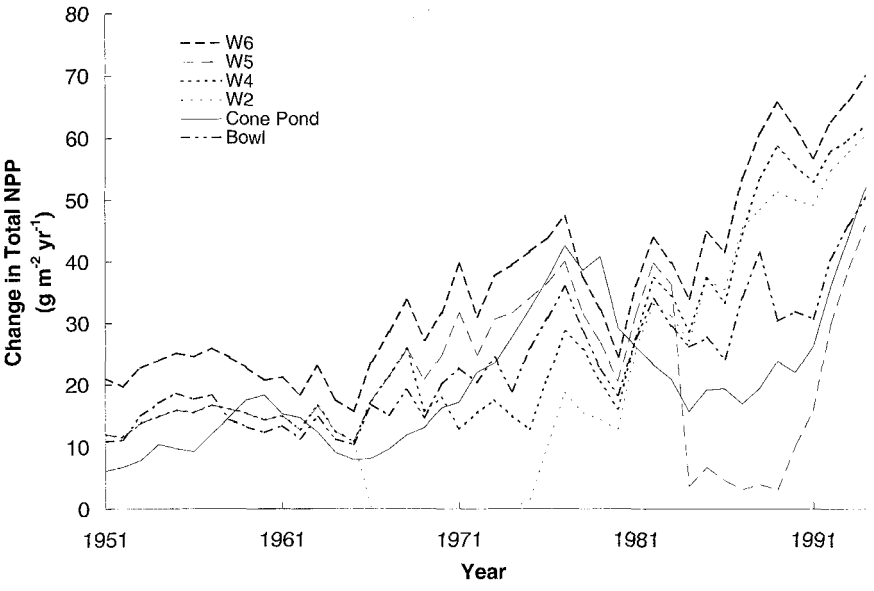


Figure 11.13. Transient PnET-CN predictions showing the difference between NPP predictions made using ambient and background levels of N deposition for six sites with different land use histories.

the temporal scales of processes such as interannual climate variability, disturbance, vegetation reestablishment, changes in C/N ratios in plant and soil compartments, and ambient N deposition overlap to produce complex patterns of C and N cycling rates.

Conclusions

PnET-II and TEM 4.0 made remarkably similar predictions of NPP under both contemporary and changed climate scenarios. That both models agreed so closely, despite their different structures and biases regarding the influence of climate variables on NPP, suggests that confidence in their predictions of forest NPP in this region should be increased, as suggested by Rastetter (1996). However, predicted responses to climate change and CO_2 enhancement varied substantially among GCM scenarios. This result suggests that further research should be directed at improving accuracy of regional-scale climate projections.

Both models predicted very large increases in forest NPP for this region under climate change and enhanced CO_2. While this is an encouraging result for policymakers attempting to balance the global C budget in the face of rising emissions, these large NPP responses are not likely to be

realized because of limitations imposed by other factors. Past land management history has depleted many sites of nutrients, such as N. In these areas, nutrient limitations will reduce potential NPP in the face of climate change. In other areas, pollutants, such as acid rain or tropospheric ozone, may impose further nutrient limitations or reduce photosynthetic potential. Finally, increased variability in precipitation is likely to induce water stress at many sites, which would further reduce forest NPP.

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Ecological Studies 139

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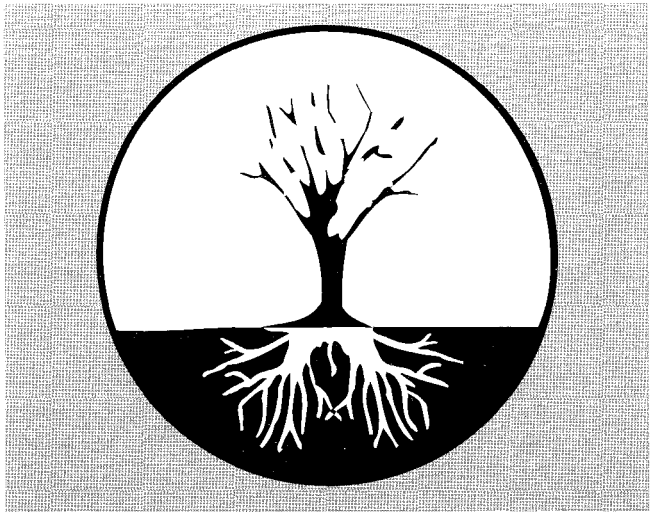

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