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Sources of Variability in Net Primary Production Predictions at a Regional Scale: A Comparison Using PnET-II and TEM 4.0 in Northeastern US Forests

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Abstract

Because model predictions at continental and global scales are necessarily based on broad characterizations of vegetation, soils, and climate, estimates of carbon stocks and fluxes made by global terrestrial biosphere models may not be accurate for every region. At the regional scale, we suggest that attention can be focused more clearly on understanding the relative strengths of predicted net primary productivity (NPP) limitation by energy, water, and nutrients. We evaluate the sources of variability among model predictions of NPP with a regional-scale comparison between estimates made by PnET-II (a forest ecosystem process model previously applied to the northeastern region) and TEM 4.0 (a terrestrial biosphere model typically applied to the globe) for the northeastern US. When the same climate, vegetation, and soil data sets were used to drive both models, regional average NPP predictions made by PnET-II and TEM were remarkably similar, and at the biome level, model predictions agreed fairly well with NPP estimates developed from field measurements. However, TEM 4.0 predictions were more sensitive to regional variations in temperature as a result of feedbacks between temperature and belowground N availability. In PnET-II, the direct link between transpiration and photosynthesis caused substantial water stress in hardwood and pine forest types with increases in solar radiation; predicted water stress was relieved substantially when soil water holding capacity (WHC) was increased. Increasing soil WHC had little effect on TEM 4.0 predictions because soil water storage was already sufficient to meet plant demand with baseline WHC values, and because predicted N availability under baseline conditions in this region was not limited by water. Because NPP predictions were closely keyed to forest cover type, the relative coverage of low- versus high-productivity forests at both fine and coarse resolutions was an important determinant of regional NPP predictions. Therefore, changes in grid cell size and differences in the methods used to aggregate from fine to coarse resolution were important to NPP predictions insofar as they changed the relative proportions of forest cover. We suggest that because the small patches of high-elevation spruce-fir forest in this region are substantially less productive than forests in the remainder of the region, more accurate NPP predictions will result if models applied to this region use land cover input data sets that retain as much fine-resolution forest type variability as possible. The differences among model responses to variations in climate and soil WHC data sets suggest that the models will respond quite differently to sce-

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narios of future climate. A better understanding of the dynamic interactions between water stress, N availability, and forest productivity in this region will enable models to make more accurate predictions of future carbon stocks and fluxes.

Key words: climate; ecosystem process modeling; modeling uncertainty; net primary production; northeastern US; PnET; soil water holding capacity; spatial resolution; TEM; vegetation representation.

INTRODUCTION

Net primary production (NPP) is the rate at which carbon (C) is accumulated by autotrophs and is expressed as the difference between gross photosynthesis and autotrophic respiration. Because rates of photosynthesis and respiration are sensitive to changes in environmental conditions caused by natural and human activities, terrestrial NPP varies across the globe and over time. Recent studies have attempted to capture the influence of spatial and temporal variability in environmental conditions on NPP at the global scale by using gridded data sets as inputs to models of the terrestrial biosphere (for example, Foley and others 1996; Kindermann and others 1996; Thompson and others 1996; Post and others 1997; Cao and Woodward 1998; Field and others 1998; Xiao and others 1998; Cramer and others 1999). However, considerable uncertainty exists in the magnitude and distribution of global NPP estimated by these models across space and time (Cramer and others 1999; Kicklighter and others 1999). This uncertainty typically is related to differences in assumed vegetation structure (Bondeau and others 1999), different sensitivities to climatic conditions (Ruimy and others 1999; Schloss and others 1999), and differences in simulation of the water balance (Churkina and others 1999) among the models.

At such broad scales, the estimates made by terrestrial biosphere models are necessarily based on broad characterizations of vegetation, soils, and climate. As a result, these models may not accurately estimate C stocks and fluxes over every region of the globe. By concentrating on a smaller portion of the globe, regional models can be developed and parameterized to simulate the carbon dynamics of a region more accurately than the terrestrial biosphere models. In addition, in regional studies the variations in local environmental conditions often can be described in greater detail by using finer-resolution data sets (for example, Sala and others 1988; Burke and others 1990, 1991, 1997; Goodale and others 1998; Ollinger and others 1998; Potter and others 1998). A comparison of NPP estimates by a global terrestrial biosphere model and a regional model can suggest areas of possible improvements in the terrestrial biosphere models to reduce uncertainty in future estimates of global NPP and carbon storage. As resource management decisions typically are made at local to regional scales (Gunderson and others 1995), a better understanding of the relationship between regional and global carbon dynamics also will help to improve our understanding of how human activities may influence the global carbon budget.

In general, discrepancies among predictions made by different models at any scale can be attributed to three sources: (a) differences in modeling assumptions and approaches (VEMAP Members 1995; Pan and others 1998; Bondeau and others 1999; Cramer and others 1999; Kicklighter and others 1999); (b) differences among input data sets in the representation of environmental conditions (Pan and others 1996); and (c) differences in the spatial resolution of input data and model results (White and Running 1994; Pierce and Running 1995; Nungesser and others 1999). To examine the importance of these sources of variability, we compared NPP estimates developed by a regional forest ecosystem process model (PnET-II) (Aber and Federer 1992) and a terrestrial biosphere model [the Terrestrial Ecosystem Model (TEM 4.0)] (McGuire and others 1995, 1997; Xiao and others 1997) for forests in the northeastern US.

Roughly 70% of the land area in the northeastern US (41 to 47.5°N, 67 to 76°W), the area chosen for this study, is forested (Lathrop and Bognar 1994). The region, however, does have a long history of agricultural use, dense human settlement, and human-induced ecological impacts (Cronon 1983; Fuller and others 1998). Accurate prediction of current NPP in this region will provide important baseline data because production and nutrient flux rates are likely to change in a future marked by changes in human settlement patterns, increasing N deposition, and climate (Aber and others 1989, 1998; Ollinger and others 1993; Magill and others 1997).

METHODS

PnET-II and TEM 4.0 use different approaches to estimate NPP, and in past applications the models have used different input data sets organized at different scales and spatial resolutions to represent

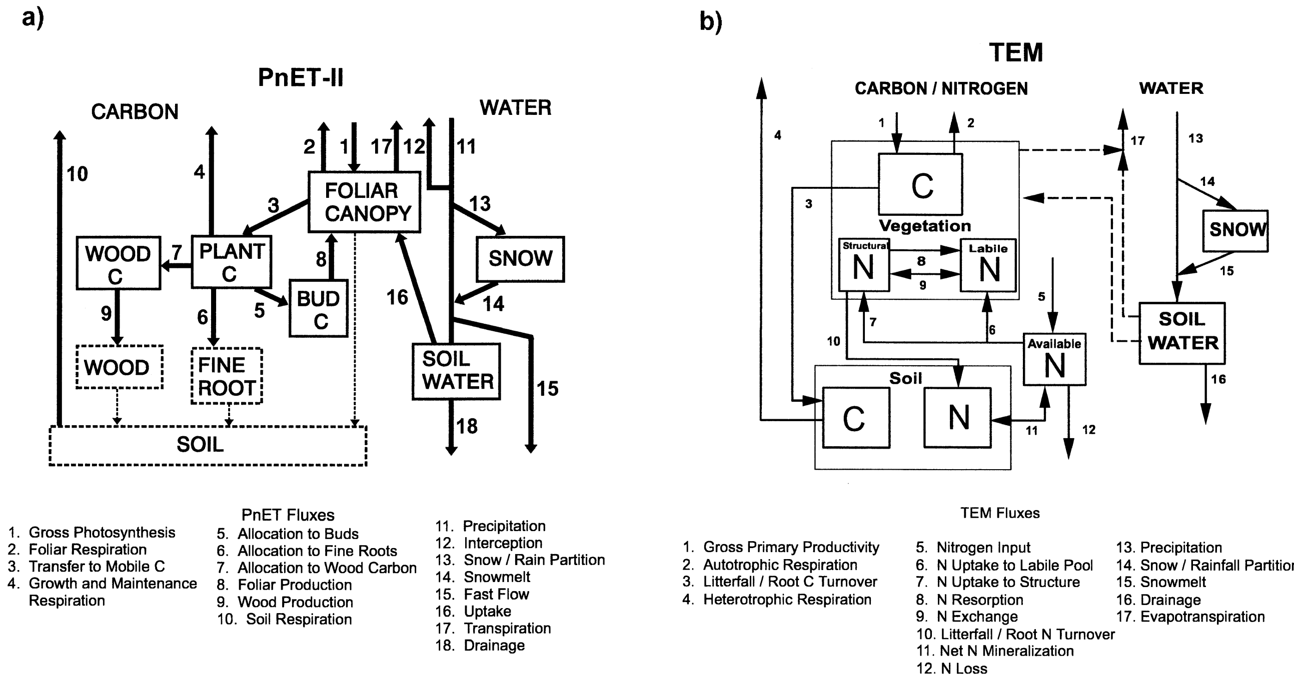

Figure 1. Comparison of PnET-II **(a)** and TEM 4.0 **(b)** model structures. Arrows indicate fluxes, and boxes indicate pools. Dashed lines indicate indirect relationships.

climate and land cover. Below, we compare the model structures, the input climate and land cover data sets, and the representation of water holding capacity (WHC) typically used by the models. We then develop a series of sensitivity experiments to examine the relative impacts of these differences on NPP estimates and to examine model responses to changes in environmental factors.

Model Descriptions

PnET-II. PnET-II (Figure 1a) is a lumped-parameter model of carbon and water dynamics in forest ecosystems. The core relationship in the model is a linear response of maximum net photosynthetic rate (A_{max}) to foliar N concentration (Field and Mooney 1986; Reich and others 1995). Conductance varies linearly with photosynthesis, such that transpiration is a function of CO_2 gain and atmospheric vapor pressure deficit. This set of simple equations results in very explicit and direct links between nitrogen status, carbon gain, and water use.

Total potential canopy photosynthesis is calculated using a numerical integration in which radiation intensity and specific leaf weight both decline with increasing canopy depth. Light is attenuated through the canopy based on the Beers-Lambert exponential decay equation ($y = e^{-k*LAI}$), leaf-specific weight declines linearly with increasing leaf area index (LAI) overhead, and carbon gain declines according to a standard asymptotic photosynthetic response curve. The result of this integration is a maximum potential net C gain for the entire canopy in the absence of water stress. Net C gain is divided into gross photosynthesis and respiration, and potential total canopy gross photosynthesis then is reduced for suboptimal conditions of temperature (symmetrical bell-shaped curve with specific optimum and minimum) and vapor pressure deficit (direct effect on stomatal conductance; minimal impact in this region). Foliar respiration is assumed to have a Q_{10} of 2.

Assuming that stomatal conductance is directly related to gross photosynthetic rate, and that internal CO_2 concentrations in C_3 plants are constant (Tanner and Sinclair 1983; Sinclair and others 1984), water use efficiency (WUE) is an inverse linear function of vapor pressure deficit (VPD) and potential transpiration is

$$\text{PotTrans} = \text{PotGrossPsn}/\text{WUE}, \qquad (1)$$

where PotTrans is transpiration in the absence of water stress and PotGrossPsn is total canopy gross photosynthesis as described above. Water stress is determined by taking monthly potential transpiration and precipitation data, integrating these gains and losses at a daily time step, and determining with a soil water release function (Aber and others 1995) whether reductions from maximum transpiration rates will occur. These are translated to reductions in stomatal conductance and hence gross photosynthesis. The sum of these daily reductions is used to reduce total monthly gross photosynthesis below the potential value calculated above.

Total canopy net photosynthesis is calculated by subtracting day and night foliar respiration, which are not affected by VPD or water stress, from gross photosynthesis. Accumulated carbon is stored in a mobile C pool (PlantC) until the end of the growing season when it is allocated to foliage (BudC), wood, and fine roots for next year's production. BudC is determined using a dynamic allocation routine that responds to interannual variability in total carbon gain. Thus, foliar production and LAI can vary year to year when actual climate time-series data are used. Whereas estimates of wood and fine root production are made, these pools do not accumulate (see PnET-CN; Aber and Driscoll 1997; Aber and others 1997). Phenology of leaf display is driven by accumulated growing degree days in the spring and by occurrence of negative carbon balances in the fall. Whereas PnET-II does not contain a complete accounting of carbon balances in wood, fine root, and soil pools, it does contain an empirical soil respiration term that can be combined with estimates of total canopy photosynthesis and wood and foliar respiration to predict net ecosystem production.

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 locations across North America (Aber and Federer 1992; Aber and others 1995) and has been tested against eddy correlation CO_2 exchange measurements (Aber and others 1996). To date, the PnET models have been applied to forests in the northeastern US at spatial resolutions of 30 arcseconds (30″) (approximately 1 km) and 0.5° (approximately 40–50 km) (Aber and others 1995; Aber and Driscoll 1997; Ollinger and others 1997, 1998; Jenkins and others 1999), to forests in the southeastern US at a spatial resolution of 0.5° (McNulty and others 1994), and to forests in Ireland at a spatial resolution of 1 km (Goodale and others 1998).

Terrestrial Ecosystem Model (TEM 4.0). Unlike PnET-II, vegetation C (both aboveground and belowground) in TEM 4.0 is simulated as a single compartment (Raich and others 1991). Atmospheric CO_2 is taken up by plants through gross primary production (GPP), and C then is respired back to the atmosphere, retained as vegetation C, or transferred to the soil C compartment as litterfall (Figure 1b).

Monthly GPP is influenced by photosynthetically active radiation (PAR), relative leaf area, air temperature, actual evapotranspiration (AET), potential evapotranspiration (PET), N availability, and atmospheric CO_2 concentration (Raich and others 1991; McGuire and others 1992, 1993, 1995, 1997; Tian and others 1999), according to the equation

$$GPP = (C_{max}) * [PAR/(k_i + PAR)] * [C_1/(k_c + C_1)] * (TEMP) * (Ac) * (KLEAF), \quad (2)$$

where C_{max} is the maximum rate of C assimilation by the entire plant canopy (under optimal conditions), k_i is the irradiance at which C assimilation is one-half of its maximum, C_1 is intraleaf (CO_2), k_c is the intraleaf (CO_2) at which C assimilation is one-half its maximum, and TEMP and Ac are multipliers describing the influence of air temperature and nitrogen availability (Raich and others 1991). KLEAF is a multiplier describing relative changes in photosynthetic capacity and is calculated separately for each month based on seasonal changes in actual evapotranspiration. The variable C_1 is the product of ambient CO_2 and a relative canopy conductance multiplier that increases monotonically with the ratio AET:PET (Pan and others 1998; Tian and others 1999). NPP is calculated as the difference between GPP and plant respiration. Monthly plant respiration is a function of air temperature and vegetation C (Raich and others 1991).

Different factors influence the PET and AET estimates in TEM than influence the transpiration terms in PnET-II. In TEM, solar radiation and temperature both are used to calculate PET (Jensen and Haise 1963). Similar to the transpiration estimates in PnET-II, AET in TEM depends on both the atmospheric demand for water (represented by PET) and the availability of soil moisture to satisfy that demand. During dry periods, the water balance model (WBM) assumes that it becomes increasingly difficult to remove soil moisture against increasing pore tension so that AET decreases rapidly at low soil moistures (Vörösmarty and others 1989). Unlike PnET-II, TEM does not consider the influence of vapor pressure deficit on stomatal conductance or photosynthesis.

Also unlike PnET-II, 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 and others 1997; Pan and others 1998; Kicklighter and others 1999). Litterfall and root turnover are simulated as a single transfer from vegetation to soil C and N pools, and N is transferred to available pools via N mineralization. Thus, N

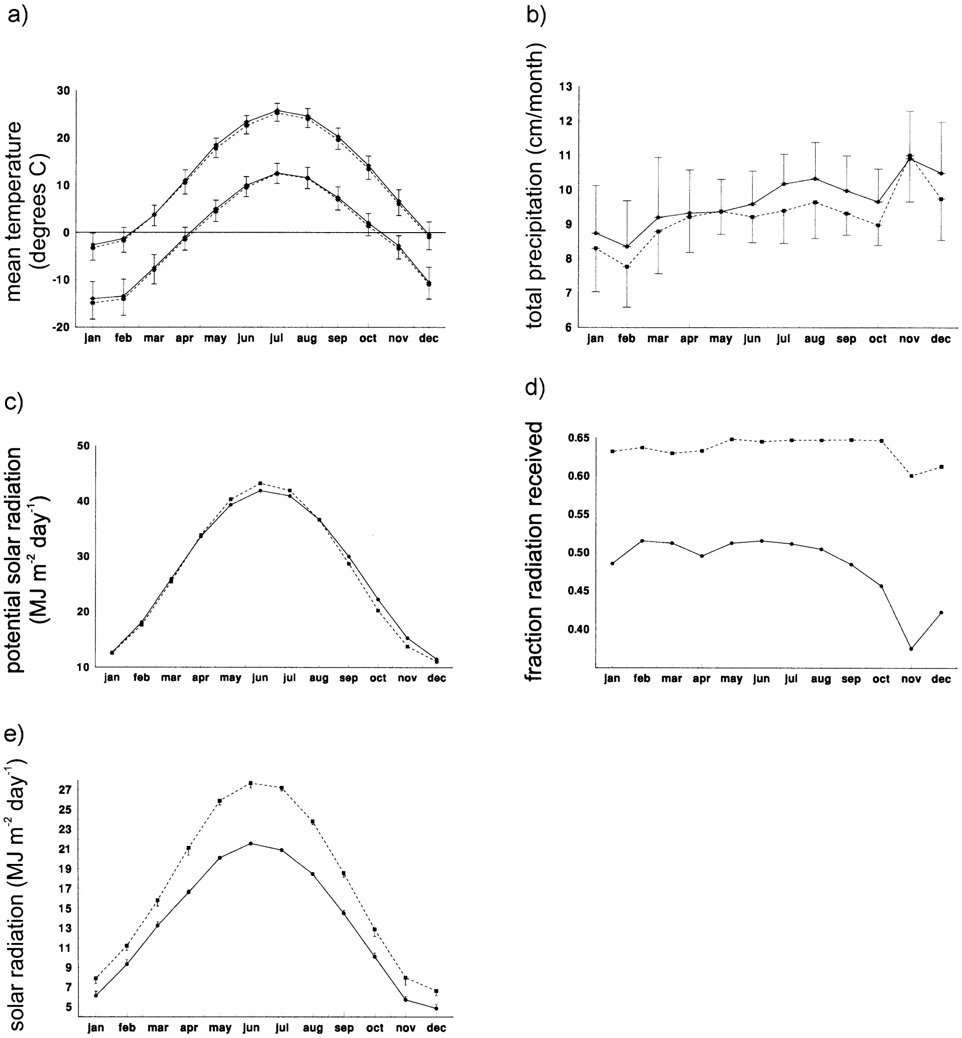

Figure 2. Comparison of climate input data sets. Climcalc (circles, solid line) and VEMAP (squares, dashed line) are plotted concurrently for comparison. All points represent the average of 115 0.5° pixels; bars are one standard deviation. **(a)** Minimum (lower line) and maximum (upper line) temperature; **(b)** total monthly precipitation; **(c)** potential radiation, determined using the algorithms of Swift (1976) for both data sets; **(d)** fraction of potential radiation received at canopy level; and **(e)** monthly mean of total daily solar radiation received at canopy level (found as potential * fraction received = net total received).

availability depends on the recycling of N from decomposing litter and soil organic matter so that seasonal rates of NPP are coupled to rates of decomposition. In contrast, PnET-II simulates a constant N availability by using a fixed foliar %N value for each forest type.

Although many of the vegetation-specific parameters in TEM 4.0 are defined from published information (Raich and others 1991; McGuire and others 1992; Melillo and others 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 used data sets gridded at a resolution of 0.5° latitude by 0.5° longitude to estimate NPP for South America (Raich and others 1991; Tian and others 1998), North America (McGuire and others 1992, 1993; VEMAP Members 1995; Pan and others 1996; Tian and others 1999), and the globe (Melillo and others 1993; McGuire and others 1995, 1997; Xiao and others 1997, 1998).

Comparison of Climate Inputs

To make NPP estimates at regional and/or global scales, both PnET-II and TEM 4.0 require gridded monthly data sets of temperature, total precipitation, and total daily solar radiation. For northeastern US simulations, PnET-II has used minimum and maximum monthly temperatures (Figure 2a), total monthly precipitation (Figure 2b), and daily solar radiation (Figure 2e) determined from latitude, longitude, and elevation by a statistical model (Climcalc) (Ollinger and others 1995). The statistical relationships in Climcalc are based on long-term (30 year) climate records for the northeastern US.

Although past applications of TEM have used a variety of climate data sets to develop NPP estimates for this region, for this study we used the VEMAP 0.5° latitude by 0.5° longitude data sets (Kittel and others 1995; VEMAP Members 1995) of minimum and maximum monthly air temperatures (Figure

2a), total monthly precipitation (Figure 2b), and net solar radiation (Figure 2e). As with Climcalc, in the VEMAP data sets elevation influences the spatial and temporal distribution of air temperatures, precipitation, and solar radiation (Marks and Dozier 1992; Daly and others 1994; Glassy and Running 1994).

Averaged regionally, monthly maximum, and minimum temperatures were almost identical between the two sets of climate data (Figure 2a). Climcalc predicted higher precipitation than the VEMAP data set for most months (Figure 2b) such that, on average, 5.35 cm y^{-1} more total precipitation occurred in the Climcalc data set than in the VEMAP data set. Although monthly potential solar radiation averaged over the region was almost identical between the two climate data sets (Figure 2c), the higher "fraction of radiation received" in the VEMAP data set (Figure 2d) caused a significant disparity in net solar radiation between the climate data sets (Figure 2e). Potential radiation is multiplied by the fraction of radiation received to obtain estimates of actual radiation received at the top of the forest canopy. In Climcalc, the fraction of potential radiation received at the ground surface is based on actual radiation measurements made across the northeastern US. These values are constant over the study region and average roughly 50%. In the VEMAP data set, the fraction of potential radiation received at canopy level is a cloud cover correction based on relationships between latitude, elevation, diurnal range of temperature, and precipitation by using algorithms of Gates (1981) and Bristow and Campbell (1984). These values average between 60% and 65%.

Comparison of Land Cover

To develop regional-scale NPP estimates, PnET-II has used a data set (Figure 3a) describing actual vegetation at 30″ spatial resolution (Aber and others 1995; Ollinger and others 1998) based on AVHRR satellite data (Lathrop and Bognar 1994). For computational efficiency, we used a version of this map aggregated to the 60″ resolution by using a pixel-thinning technique (Figure 3a). TEM 4.0 has used several potential vegetation data sets at 0.5° spatial resolution to estimate NPP in this region, but for this study we use the VEMAP potential vegetation data set (Kittel and others 1995) based on Küchler (1964, 1975) (Figure 3c).

In addition to their differences in spatial resolution, the two land cover data sets also use different classification schemes. The AVHRR classification

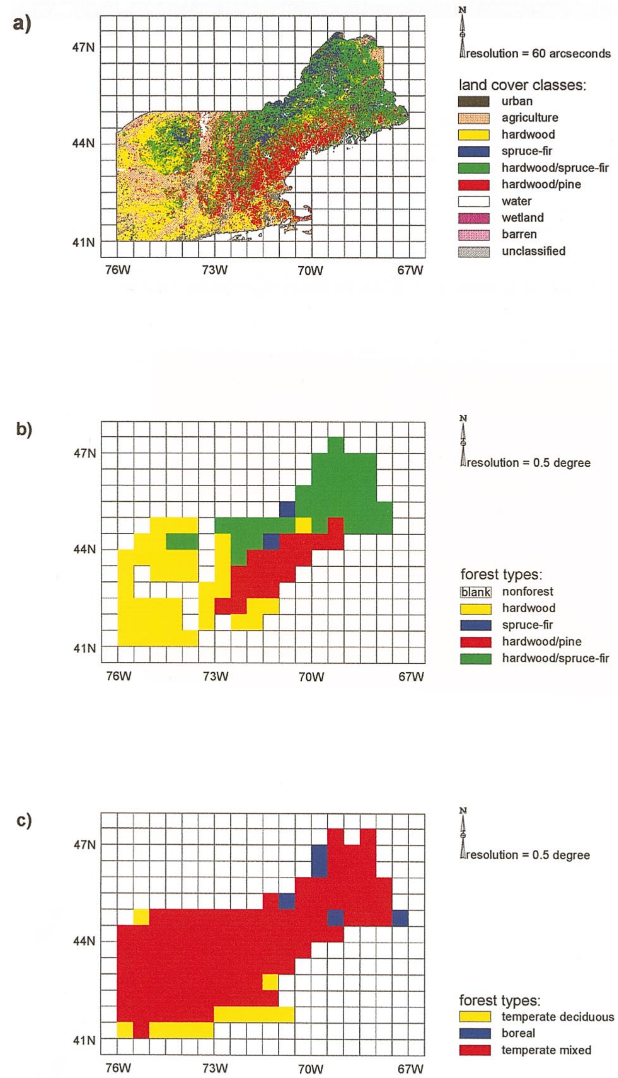

Figure 3. (a) AVHRR-generated land cover map at 60″ resolution; (b) dominant land cover map developed from 60″ resolution map; and (c) potential vegetation map used in the VEMAP activity (VEMAP Members 1995).

identified four forest types in the region (Figure 3a): hardwood, spruce-fir, hardwood/spruce-fir, and hardwood/pine. Based upon USDA Forest Service Forest Inventory and Analysis data (Beltz and others 1992), hardwood/spruce-fir pixels were assumed to be 40% hardwood and 60% spruce-fir, whereas hardwood/pine pixels were assumed to be 60% hardwood and 40% pine.

The VEMAP classification identified three forest types in the region: boreal, temperate deciduous, and mixed temperate forests. TEM used the parameterizations for these forest types described by VEMAP Members (1995), in which mixed temperate forests were assumed to be a 50:50 mixture of temperate deciduous and temperate continental

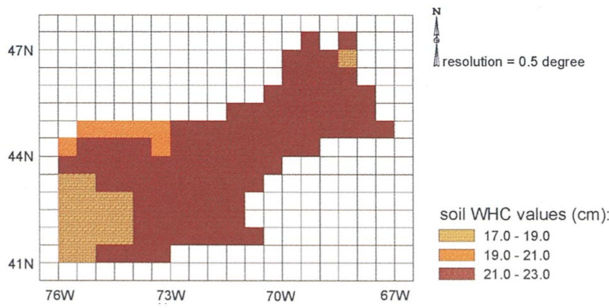

Figure 4. TEM WHC data set. See text for descriptions of model simulations using this as model input.

Table 1. Structure of Model Comparisons

	Input Variables			
Comparisons	Land Cover Data Set	Soil WHC	Climate Data Set	Spatial Resolution
Baseline	Dominant	12 cm	Climcalc	*0.5°*
Climate data set	Dominant	12 cm	*VEMAP*	0.5°
Soil WHC	Dominant	*TEM*	Climcalc	0.5°
Land cover data set	*Mosaic*	12 cm	Climcalc	0.5°
	Vemap	12 cm	Clincalc	0.5°
Spatial resolution	Dominant	12 cm	Climcalc	**60″**

Input variables were changed one at a time, and model results were compared with the baseline run. Input variables changed from the baseline are italicized.

coniferous forests. To use PnET-II with the VEMAP classification scheme, we parameterized boreal forests as spruce-fir, temperate deciduous forests as hardwoods, and temperate mixed forests as equal parts hardwood and pine.

Comparison of WHC

PnET-II and TEM 4.0 both use the concept of soil WHC (defined as field capacity minus wilting point) to represent the maximum amount of water that can be stored and made available to plants. PnET has assumed a constant 12 cm WHC in all New England analyses to date (Aber and Federer 1992; Aber and others 1995, 1997; Jenkins and others 1999); the 12 cm WHC value is based on an assumed rooting depth of 1 m and the 25% coarse fragments typically encountered in well-drained till soils in northeastern forests (Ollinger and others 1998). In contrast, the WBM linked with TEM uses vegetation type and soil texture to determine rooting depth and WHC for each grid cell (McGuire and others 1997; Xiao and others 1997). For the northeastern US (Figure 4), TEM estimates that WHC ranges from 17.0 to 22.5 cm (41% to 88% higher than the constant 12 cm), with a regional average of 21.4 ± 1.8 cm.

Design of the Sensitivity Experiments

The differences described above provided an opportunity to examine the sensitivity of the two models to changes in a variety of environmental factors, and to explore the uncertainty associated with different methods of scaling up from fine resolution data. For example, two approaches can be used to aggregate from fine to coarse resolution by using vegetation data. In one commonly used approach, a single "dominant" forest type is assigned to a coarse resolution grid cell based on the relative occurrence of that forest type within the grid cell. A second approach is to conduct model simulations on all the different vegetation types found within a coarse grid cell and then weigh the contribution of the various vegetation types at the coarser resolution based on the relative proportion of the vegetation type (a "mosaic vegetation" approach). The latter approach retains more fine resolution information at the coarser resolution. A recent study (Kicklighter and others 1999) has found large differences in NPP estimated by two models that used the same functional formulations, but were parameterized to vegetation data sets that used different classification schemes. To explore these issues, we developed five sensitivity experiments (Table 1) to examine the effects on NPP estimates of using (a) different climate data sets; (b) different approaches for representing soil properties; (c) different methods of representing vegetation within a grid cell (that is, dominant versus a mosaic of forest types); and (d) different spatial resolutions to develop regional NPP estimates. The experiments were performed by changing one variable at a time, and the resulting NPP estimates were compared with results from a baseline run. Comparisons between model estimates were performed at the 0.05 significance level by using Wilcoxon Signed Rank tests (due to nonnormal distribution of sample data) by using Systat 7.0 (SPSS Corp., Chicago, IL).

Baseline Run. We developed baseline NPP estimates by using climate data from the Climcalc model at 0.5° resolution; a dominant forest cover data set derived from an aggregation of the AVHRR data to 0.5° resolution (Figure 3b); and the assumption of a constant 12 cm WHC across the region. To calculate air temperatures, precipitation and solar radiation at 0.5° spatial resolution, Climcalc used

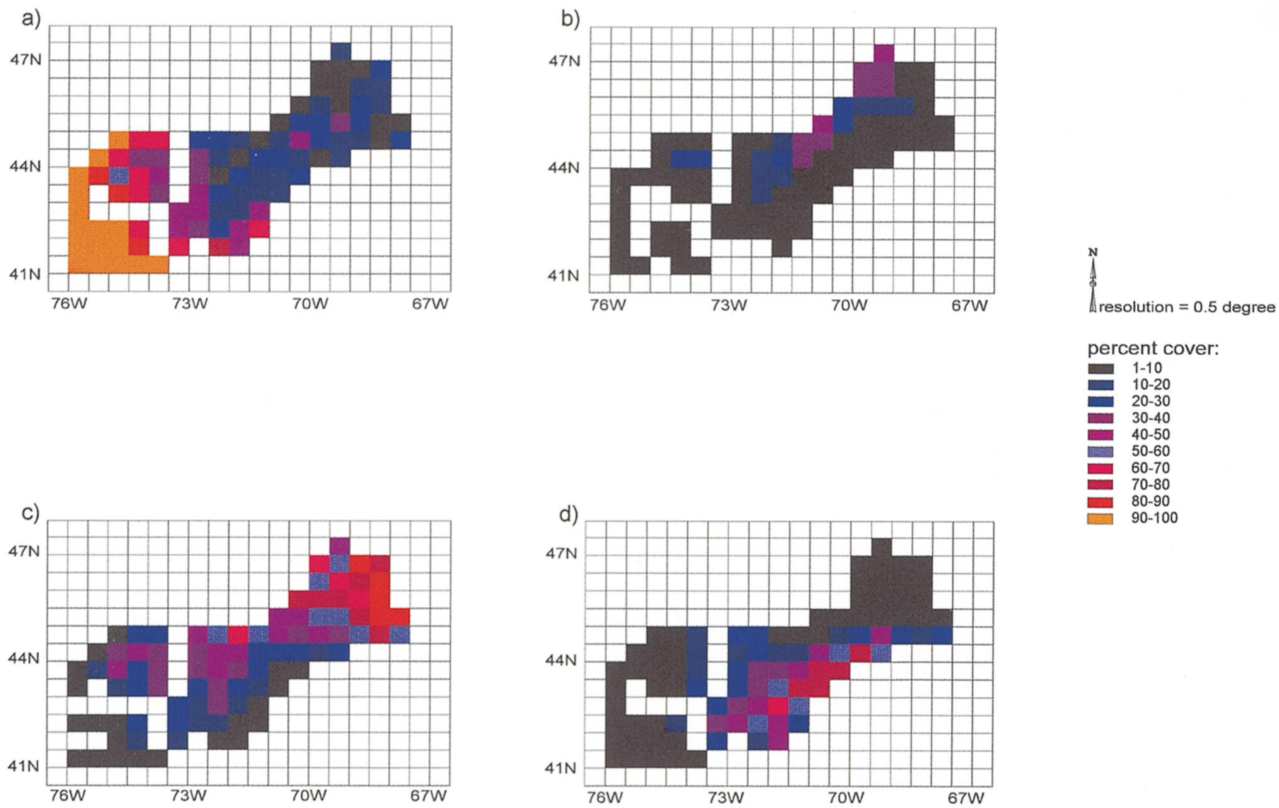

Figure 5. Mosaic land cover maps at 0.5° resolution. See text for aggregation method. (**a**) Percent hardwood; (**b**) percent spruce-fir; (**c**) percent hardwood/spruce-fir; and (**d**) percent hardwood/pine.

the digital elevation model (DEM) included in the VEMAP database (VEMAP Members 1995). We excluded from the analysis any 0.5° grid cell with less than 50% total forest cover. The resulting region consisted of 115 0.5° grid cells, 94 forested and 21 nonforested.

To use TEM with the AVHRR classification scheme, we parameterized hardwoods as temperate deciduous forests, spruce-fir forests as boreal, hardwood/spruce-fir forests as a mixture of 40% temperate deciduous and 60% boreal, and hardwood/pine forests as a mixture of 60% temperate deciduous and 40% continental temperate coniferous.

To develop baseline NPP estimates from TEM by using constant soil properties, we assumed a loam soil texture for all soils in the northeastern US. In addition, we modified TEM slightly to constrain soil WHC to a constant 12 cm across the region.

Experiment 1: Sensitivity of NPP to the Representation of Climate. We developed NPP estimates from PnET-II and TEM at 0.5° resolution by using the climate data from the VEMAP comparison, the baseline dominant forest cover map, and the constant 12 cm soil WHC. These estimates were compared with the baseline predictions developed using Climcalc to examine the influence of using different climate data sets.

Experiment 2: Sensitivity of NPP to the Representation of Soil WHC. To examine the influence of different assumptions about soil properties, we first developed a regional soil WHC data set by using the WBM algorithms in TEM with the VEMAP soil texture data set (VEMAP Members 1995) for input to PnET-II (Figure 4). We then developed NPP estimates from both models by using the spatially explicit TEM WHC data set, the baseline climate data sets, and the baseline dominant forest cover data set. NPP estimates derived using this variable WHC data set were compared with those derived during the baseline estimates by using the constant 12 cm.

Experiment 3: Sensitivity of NPP Estimates to the Coarse-Resolution Representation of Vegetation. We determined the proportion of forested land covered by each of the four forest types in each 0.5° grid cell based on the forest classification of the 60″ grid cells (Figure 5). We then ran PnET-II and TEM four times for each 0.5° grid cell (that is, once for each forest type) and added the results together to obtain NPP estimates for that 0.5° grid cell based on the proportional cover of each of the four forest types (that is, a mosaic of forest types). In each of the model runs, we used the baseline climate data sets and the

Table 2. Results from Sensitivity Experiments

	Comparison Tested[a]									
	Baseline[b]		Climate[b]		Soil WHC[b]		Dominant vs Mosaic[b]		Spatial Resolution[c]	
	PnET-II	TEM 4.0	PnET-II	TEM 4.0	PnET-II	TEM 4.0	PnET-II	TEM 4.0	PnET-II	TEM 4.0
Average[d]	1118.5	1243.2	1203.3	1221.2	1248.4	1237.5	1094.0	1206.7	1084.2	1194.0
SD	185.7	308.4	166.0	329.2	252.8	283.1	152.8	287.3	195.3	291.3

All values reported are NPP, in units of gOM m^{-2} y^{-1}.
[a]*See Table 1 for structure of model comparisons.*
[b]*n = 94.*
[c]*n = 76,425.*
[d]*Calculated as the average for forested grid cells in the region.*

constant 12-cm soil WHC. We compared these estimates with those developed using the baseline dominant forest cover data set to examine the implications of this "mosaic" approach to spatial aggregation of land cover data.

Experiment 4: Sensitivity of NPP Estimates to Differences in Spatial Resolution. We used PnET-II and TEM 4.0 to develop model predictions by using the AVHRR-derived land cover data at 60″ resolution, climate data calculated from Climcalc with a 60″ DEM, and the constant 12 cm soil WHC. Model predictions at 60″ were generated using only those grid cells classified as forest (that is, a total of 76,425 grid cells). These high-resolution predictions were compared with results from the baseline run at 0.5° resolution to examine the influence of spatial resolution on regional NPP estimates.

Results

In the baseline run and all of the sensitivity experiments, the mean annual NPP estimated for the northeastern US by PnET-II and TEM 4.0 did not differ by more than 11% (Table 2). Although these differences in NPP estimates often were statistically significant, they were well within the measurement error associated with the field measurement of NPP. The standard deviations of annual NPP estimated by TEM in all model runs, however, indicated a larger variability of NPP estimates across the region than PnET-II. In addition, the models responded differently to many of the changes imposed in the sensitivity experiments. Below, we examine how these responses are related to model structure and assumptions.

Baseline NPP Predictions

For the northeastern US, the regional average NPP predicted by TEM 4.0 for the baseline run (1243.3 gOM m^{-2} y^{-1}) was significantly greater than the corresponding PnET-II prediction (1118.5 gOM m^{-2} y^{-1}; Table 2; $P < 0.0005$), although these baseline predictions were within 10% of each other. The range of TEM 4.0 predictions (610.9–1805.3 gOM m^{-2} y^{-1}) was approximately 1.75 times the corresponding range of PnET-II predictions (718.3–1399.1 gOM m^{-2} y^{-1}). Similar to Bondeau and others (1999), we found that the NPP estimates of both PnET-II and TEM 4.0 depended heavily upon the vegetation type prescribed for a grid cell (Figure 6a).

TEM predicted higher NPP than PnET-II for most hardwood and mixed hardwood/pine grid cells. Previous sensitivity analyses have shown that in the northeast region, PnET-II NPP predictions in hardwood and pine forest types correlate more closely with precipitation ($r^2 = 0.46$ and 0.27 in hardwood and pine forests, respectively; Ollinger and others 1998) than with any other climate or soil input variable. In contrast, the NPP estimates made by TEM are not as sensitive to precipitation in this region. This difference in sensitivity to water stress is partially related to differences in model parameterization. However, PnET-II does include a drainage term (FastFlowFrac), which directs 10% of water inputs to drain immediately via macropore flow (Aber and Federer 1992). Because TEM includes no such term, PnET-II simulates drier forest soils than TEM for the same precipitation input. TEM NPP predictions in this region are most clearly limited by temperature and growing degree-days GDD (Jenkins and others 1999) suggesting that feedbacks between belowground N availability and temperature are the most important controllers of predicted productivity in the northeast.

For spruce-fir forests, TEM predicted substantially lower NPP than PnET-II. TEM parameterized spruce-fir forest for this study with information from a

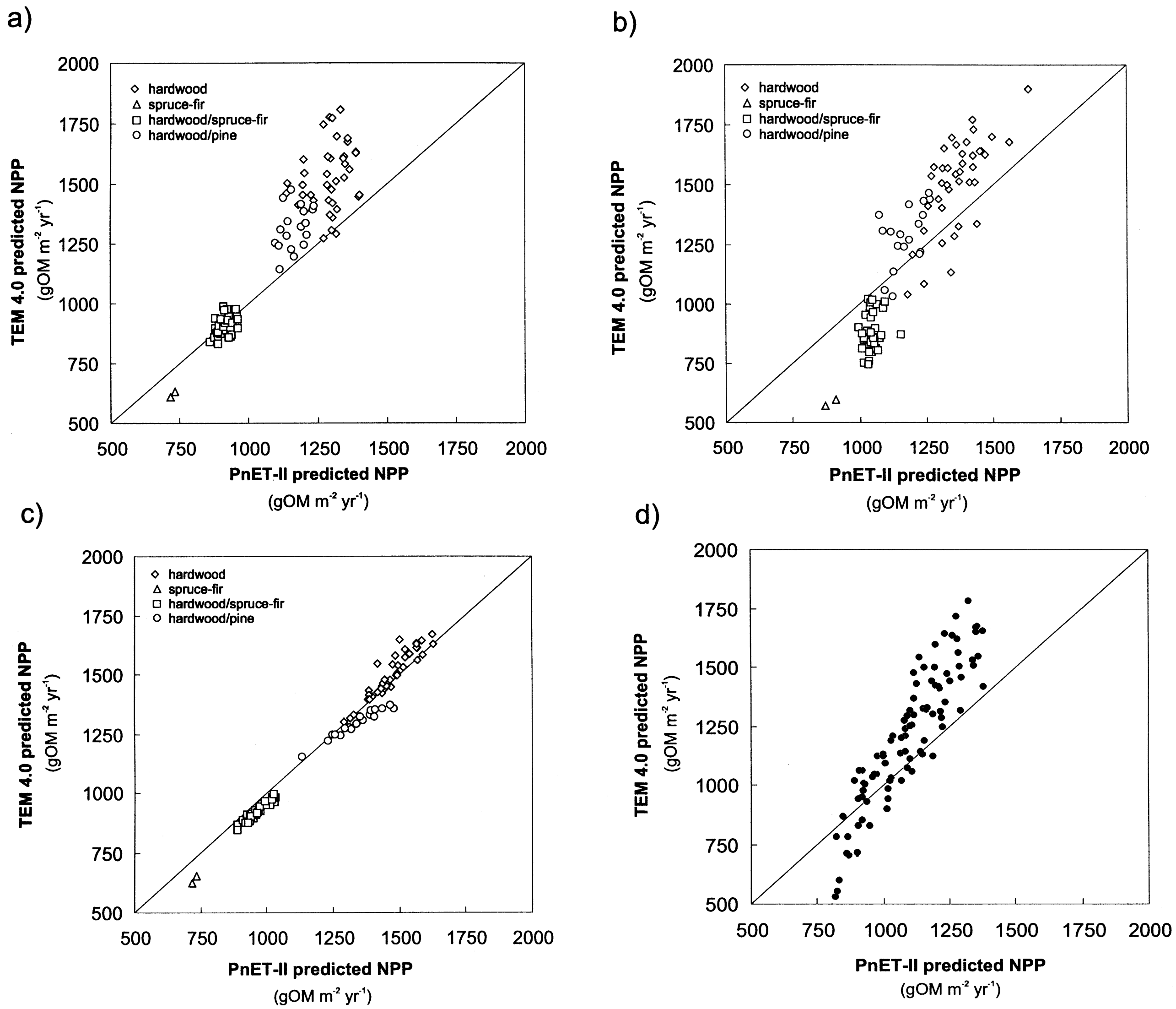

Figure 6. Comparison of TEM 4.0 vs PnET-II NPP predictions from: (**a**) baseline run; (**b**) model runs using VEMAP climate data instead of the Climcalc climate data; (**c**) model runs using a variable WHC instead of a constant 12-cm WHC; and (**d**) model runs using the mosaic land cover data set instead of the dominant land cover data. Each point represents one of the 94 forested pixels included in the dominant land cover map.

boreal forest site in Alaska (McGuire and others 1992). As the spruce-fir forests in the northeastern US grow at the southern edge of the boreal forest range, the use of Alaskan forest for calibration may have caused a lower estimate for the northeast region than is appropriate. However, spruce-fir forests make up a very small percentage of land area in the northeast, so the average NPP estimated by TEM 4.0 for the region was still higher than the average NPP estimated by PnET-II. Because spruce-fir forests are not water limited under normal conditions as simulated by PnET-II, foliar N content is the most important driver of predicted NPP in this forest type (Ollinger and others 1998). For TEM, temperature and nitrogen availability are again the most important factors influencing NPP in spruce-fir forests (Melillo and others 1993; Xiao and others 1997).

Whereas interactions among precipitation, GDD, and N availability are critical to forest productivity as simulated by both models (Ollinger and others 1998; Jenkins and others 1999), the relative strengths of these limitations on productivity differ by model and forest type. TEM appeared to be more sensitive to spatial and seasonal variations in the baseline climate than PnET-II. The positive feedback between N availability and GDD, combined with differences in parameterization for the different forest types, explains the larger range in the baseline

TEM predictions for this region (Figure 6a). The direct link between photosynthesis and transpiration causes PnET-II to be more sensitive to water stress; this constraint on NPP as simulated across the region narrows the range of baseline PnET predictions.

Sensitivity of NPP Estimates to the Representation of Climate

Unlike the baseline NPP estimates, differences between NPP predictions made by the two models under the VEMAP climate (Table 2) were not statistically significant ($P < 0.381$). The enhanced solar radiation and slightly lower precipitation in the VEMAP data set caused PnET-II to predict an increase in photosynthesis that outweighed the increase in predicted water stress. Conversely, TEM 4.0 predicted an increase in water stress that outweighed the potential gains in photosynthesis.

PnET-II uses PAR to calculate the rate of gross photosynthesis. In the model, enhanced radiation will affect the water balance indirectly if additional photosynthesis and associated transpiration are sufficient to induce water stress. As discussed above, from previous sensitivity analyses with PnET-II, we have found that in this region, precipitation and soil WHC are critical for predicting NPP in hardwood and pine forests but are less important for spruce-fir (Ollinger and others 1998). Because spruce-fir forests were not already water limited as simulated by PnET-II, the increased solar radiation under the VEMAP climate caused an increase in spruce-fir NPP (Figure 6b), which was not offset by water stress, despite the slightly lower precipitation in the VEMAP climate.

Hardwood NPP estimated by PnET-II increased very slightly under the VEMAP climate. This suggests that in the water-limited hardwood forest, the increase in photosynthesis due to additional solar radiation was offset by the additional water stress induced by increased transpiration and lower precipitation. The increases in hardwood/spruce-fir NPP were intermediate between those in the spruce-fir and the hardwood forest types and were most likely a result of the 40:60 mixture of hardwood–spruce-fir in the mixed pixels. The decrease in predicted NPP under the VEMAP climate for mixed hardwood/pine forests suggests that the additional photosynthesis combined with lower precipitation induced additional water stress in both forest types, resulting in an overall decrease in PnET-II predictions of NPP.

As PET increases with enhanced solar radiation in TEM, the AET:PET ratio decreases, so an increase in radiation can cause an increase in water stress. However, PAR also is positively related to GPP in TEM. For the northeast US, the radiation-induced water stress (combined with the slightly lower precipitation) had a larger effect on NPP than the enhancement of photosynthesis by increased PAR. As a result, predicted NPP was lower in many grid cells under the VEMAP than the Climcalc climate (Figure 6b). This result is similar to that of Pan and others (1996), who reported that an increase in solar radiation caused a decline in TEM-predicted NPP at the continental scale.

Sensitivity of NPP Estimates to Soil WHC

PnET-II predicted slightly higher regional average NPP than TEM 4.0 using the TEM WHC data set (Table 2). While statistically significant ($P < 0.009$), the difference between the model predictions was smaller than 1%.

Enhanced soil WHC decreases total drainage and increases the amount of water available to meet transpirational demand in PnET-II, thereby partially relieving water stress and directly increasing photosynthesis and NPP. PnET-II predicted a statistically significant increase in NPP under the variable WHC ($P < 0.0005$) of roughly 12% (Table 2), primarily as a result of reduced water stress in hardwood and hardwood/pine forests. Predicted NPP in the two grid cells comprising the spruce-fir forest did not respond to increased WHC (Figure 6c), providing further evidence that predicted photosynthesis in this forest type is slow enough that it is not normally limited by transpirational demand. The increased production of the hardwood/spruce-fir pixels by using PnET-II under the TEM WHC is a result of increases in NPP attributable to reduced water stress in the hardwood portion of those mixed pixels.

In TEM, enhanced soil WHC allows soils to support higher rates of AET and net N mineralization during dry periods of the year (that is, months when precipitation inputs are less than the atmospheric demand for water as represented by PET). TEM 4.0 predicted a very slight decline in average regional NPP from the baseline run when the TEM WHC data set was used, though the change was not significant ($P < 0.928$). TEM's failure to respond substantially to enhanced WHC suggests that in the model (a) soil water storage under the constant 12 cm WHC was already sufficient to meet the PET demand estimated by the WBM; and (b) N availability for plant growth is not limited by water in this region.

Sensitivity of NPP Estimates to the Representation of Vegetation

When the mosaic forest cover map was used to develop NPP estimates, predictions made by both models decreased slightly ($P < 0.0005$ and $P < 0.011$ for PnET-II and TEM 4.0, respectively; Table 2). The decline in predicted NPP under the mosaic forest cover data set occurred because the mosaic data set, which takes into account the small patches of spruce-fir forest at high elevations and northern latitudes, allocated a higher proportion of its cover to less productive forest types (that is, spruce-fir) at the expense of more productive types (that is, hardwood and hardwood/pine). The overall decline in regional average NPP was more pronounced for TEM because that model predicted substantially lower NPP in spruce-fir forests than PnET-II. However, the average NPP estimated by TEM 4.0 for the region was still higher than the average NPP estimated by PnET-II, because spruce-fir forests make up a small percentage of the land area in the northeast.

The use of the mosaic land cover data set removed the clustering of predicted NPP within forest types (Figure 6d). As a result, the continuum of grid cell NPP estimates better reflected the distribution of NPP across the region than was possible with the use of a dominant vegetation type. This underlines an important point: because these models are keyed closely to land cover type, the accuracy of forest cover classification is critical to achieving accurate NPP predictions at broad scales.

Sensitivity of NPP Estimates to Differences in Spatial Resolution

At the 60″ spatial resolution, the average NPP estimated by both models was again slightly lower, but statistically different from the baseline estimates at 0.5° resolution (Table 2) ($P < 0.0005$ for both PnET-II and TEM 4.0). Similar to the experiment using a mosaic of forest types, the reduced NPP at fine resolution occurred because small patches of spruce-fir forest were included in the land cover data set at 60″ but excluded at 0.5° resolution. However, better consideration of the lower temperatures associated with high elevations in the 60″ resolution data set caused NPP estimates by both PnET-II and TEM 4.0 to be smaller than the corresponding estimates from the mosaic vegetation experiment. Whereas the difference between mean NPP predictions made by the two models at the 60″ resolution was less than 10% (1084.2 and 1194.0 gOM m^{-2} y^{-1} for PnET-II and TEM 4.0, respectively), the difference was statistically significant ($P < 0.0005$).

Discussion

The similarities in NPP estimates between PnET-II and TEM 4.0 suggest that terrestrial biosphere models can adequately represent NPP in the northeastern US for studies of global carbon dynamics under contemporary conditions. However, our results suggest that terrestrial biosphere models will overestimate NPP in the northeastern US if such studies are based on dominant forest types at the 0.5° spatial resolution because the influence of the less productive spruce-fir forests occurring at high elevations on regional NPP estimates is not considered. Better NPP estimates can be obtained from these models at the 0.5° resolution for this region if a mosaic of forest types within a grid cell is considered when developing regional NPP estimates.

Differences in the NPP responses of PnET-II and TEM to the different climate and water holding capacity data sets suggest that these models will predict different forest responses to future climate change (see Jenkins and others 1999). Terrestrial biosphere models might not accurately predict future NPP in a given region even though contemporary NPP conditions are adequately represented; the uncertainty about trajectories in future forest productivity is related to different assumptions about the relative strengths of energy, water, and nutrient limitations on productivity in forests. Such differences are not inherently the result of using a regional model or a terrestrial biosphere model, but they may be resolved through comparisons like this one, in which regional-scale predictions are examined carefully to determine the sources of model variability. For example, in this analysis the difference in water stress simulated by the two models is based primarily on differences in basic assumptions about the important factors controlling transpiration and evaporation in forests, but the impacts of the model assumptions were only apparent when the same input data sets were used to drive both models.

Several additional terrestrial biosphere models have developed NPP estimates for this region. If we select the NPP estimates of Biome-BGC (Hunt and Running 1992; Running and Hunt 1993), Century (Parton and others 1987, 1988, 1993), and TEM 4.0 of the appropriate grid cells from the VEMAP predictions for contemporary conditions (VEMAP Members 1995; Schimel and others 1997) and compare them with the NPP estimates of PnET-II using the VEMAP potential vegetation, climate, and soil texture/WHC data sets, we find that the predictions made by PnET-II and TEM 4.0 are more similar to each other than to the predictions by Century or BIOME-BGC (Table 3). For the temperate mixed forest, which comprised 85% of the land area, the highest regional total NPP predicted by BIOME-BGC was more than double the corresponding prediction made by Century. We suggest that the

Table 3. Comparison of NPP Results with VEMAP Models

Land Cover Map	Climate	Forest Type	Model[a]	Regional NPP (Tg OM y^{-1})	Total Area (km^2)	Area-Weighted Mean NPP (gOM m^{-2} y^{-1})
VEMAP	VEMAP	boreal forest[b]	BBGC	24.4		2252.0
			CENT	20.0	10,815	1851.2
			PnET	10.0		926.4
			TEM	7.0		645.7
VEMAP	VEMAP	temperate mixed[c]	BBGC	415.9		1909.9
			CENT	202.0	217,729	928.0
			PnET	260.1		1194.5
			TEM	243.1		1117.1
VEMAP	VEMAP	temporate deciduous[d]	BBGC	55.7		2017.9
			CENT	32.5	27,592	1177.3
			PnET	39.4		1426.2
			TEM	43.5		1578.7
VEMAP	VEMAP	TOTAL	BBGC	495.9		1936.0
			CENT	254.5	256,136	993.7
			PnET	309.4		1207.0
			TEM	293.6		1146.7

[a]*BBGC, Biome-BGC; CENT, CENTURY; PnET, PnET-II; TEM, TEM 4.0.*
[b]*Run using spruce-fir parameter values.*
[c]*Run assuming 50% pine and 50% hardwood forest cover.*
[d]*Run assuming 100% hardwood forest cover.*

differences among the VEMAP models at the regional scale of this analysis were driven by differing model assumptions about the relative strengths of NPP limitation by nutrients, water, and energy in this region (sensu VEMAP Members 1995).

Comparisons with Measured Data

To evaluate our model predictions, we compared the NPP estimates described above with field-measured NPP data from forests in this region. Aboveground NPP estimates described in the field studies were transformed to correspond to total NPP, as predicted by the models, by assuming that root production was equal to annual aboveground litterfall, as suggested by Raich and Nadelhoffer (1989). For temperate mixed forests, which cover most of this region, the NPP estimates of Century, PnET-II, and TEM 4.0 are consistent with total NPP determined from field studies at Harvard Forest in Petersham, Massachusetts although the Century estimates tend to be low (Figure 7). NPP estimates from Biome-BGC are almost twice the field measurements in this forest type. For boreal and temperate deciduous forests, the correspondence between model NPP estimates for the region and field measurements is not as good. The modeled NPP estimates based on the five boreal grid cells in the VEMAP vegetation data set are either too high (Biome-BGC and Century) or too low (PnET-II and TEM 4.0) compared with field measurements at

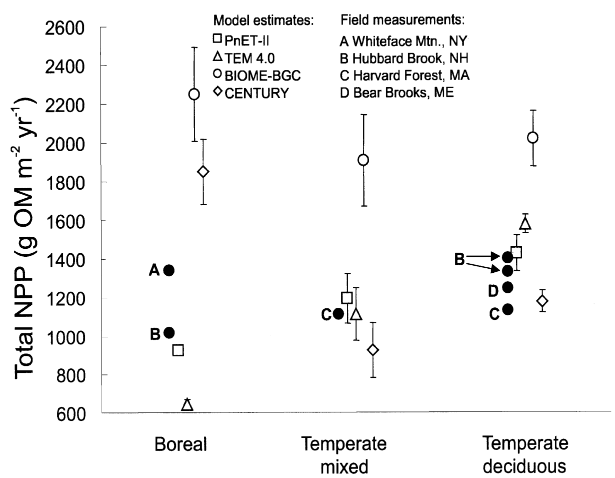

Figure 7. Comparison of model NPP predictions for the New England region against field-measured NPP data. Total NPP estimates were developed from reported aboveground NPP measurements as described in the text. Data points are offset slightly for clarity. Data sources are as follows: A, Whiteface Mountain, NY (Sprugel 1984); B, Hubbard Brook, NH (Whittaker and others 1974); C, Harvard Forest, MA (Aber and others 1993); D, Bear Brooks, ME (Magill and others 1996).

Whiteface Mountain, New York and Hubbard Brook, New Hampshire. With the exception of Century, the NPP estimates based on the 12 temperate deciduous forest grid cells in the VEMAP vegetation data set are all higher than field measurements at Bear Brooks, Maine, Hubbard Brook, or Harvard Forest. This most likely occurred because the sites where field measurements were taken are located somewhat to the north of the temperate deciduous pixels in the VEMAP land cover data set, such that climatic constraints on field-measured production would cause differences between measured and modeled NPP. In this analysis, note that information from studies at Harvard Forest has been used to calibrate TEM 4.0. Similarly, some input parameters for PnET-II were developed from studies conducted at these field sites.

Additional validation data sets are required to better assess the accuracy of these models relative to field-measured data. To determine unequivocally that a model makes accurate predictions for a particular field site, however, one must collect data from all of the components (that is, aboveground, belowground, and foliar production) of NPP along with the concurrent climatic, physiographic, and land use history conditions at that site. Whereas the difficulty of finding an appropriate match between field-collected data and model predictions does not invalidate the use of field-collected data for assessment of model performance under contemporary conditions, it does point to the need for development of biomass and NPP estimates by using broad-scale forest growth databases at resolutions appropriate for comparison with models. We currently are developing such a database at the continental scale, by using the Forest Inventory and Analysis (FIA) data collected by the USDA Forest Service at five- to 15-year intervals to estimate forest NPP on a spatially explicit basis. Though these data are not without flaws, the FIA data set remains the most comprehensive, complete, and reliable long-term data set of forest growth available for the US.

Conclusions

Our comparison of the results of a regional model (PnET-II) and a terrestrial biosphere model (TEM 4.0) indicates that terrestrial biosphere models can adequately represent NPP of undisturbed forests in the northeastern US under contemporary conditions. However, these estimates can be improved by (1) representing land cover as a mosaic of vegetation types derived from finer resolution data instead of as a single dominant vegetation type in large grid cells; and (2) having a better understanding of the effects of water stress on N availability and forest productivity in this region. The latter improvement is especially important for the ability of terrestrial biosphere models to represent adequately future NPP in undisturbed forests in the region.

Whereas models run at continental scales may not represent NPP accurately in every smaller region, modeling at these scales provides an important framework within which to understand global C stocks and fluxes. At the regional scale, the effects of human settlement patterns, forest management, and policy decisions on carbon fluxes and storage can be represented in greater detail. Few models at any scale are capable of incorporating explicitly the impacts of land-use history and secondary succession on ecosystem processes, and even fewer gridded data sets of land-use history and successional status are currently available. As interest grows in quantifying C fluxes across the landscape and the globe, the results of regional modeling of the impacts of human land use can help to improve global modeling efforts under current and future conditions.

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