



Estimating regional forest productivity and water yield using an ecosystem model linked to a GIS

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Abstract

We used the PnET-II model of forest carbon and water balances to estimate regional forest productivity and runoff for the northeastern United States. The model was run at 30 arc sec resolution (approximately 1 km) in conjunction with a Geographic Information System that contained monthly climate data and a satellite-derived land cover map. Predicted net primary production (NPP) ranged from 700 to 1450 g m⁻² yr⁻¹ with a regional mean of 1084 g m⁻² yr⁻¹. Validation at a number of locations within the region showed close agreement between predicted and observed values. Disagreement at two sites was proportional to differences between measured foliar N concentrations and values used in the model. Predicted runoff ranged from 24 to 150 cm yr⁻¹ with a regional mean of 63 cm yr⁻¹. Predictions agreed well with observed values from U.S. Geologic Survey watersheds across the region although there was a slight bias towards overprediction at high elevations and underprediction at lower elevations.

Spatial patterns in NPP followed patterns of precipitation and growing degree days, depending on the degree of predicted water versus energy limitation within each forest type. Randomized sensitivity analyses indicated that NPP within hardwood and pine forests was limited by variables controlling water availability (precipitation and soil water holding capacity) to a greater extent than foliar nitrogen, suggesting greater limitations by water than nitrogen for these forest types. In contrast, spruce-fir NPP was not sensitive to water availability and was highly sensitive to foliar N, indicating greater limitation by available nitrogen. Although more work is needed to fully understand the relative importance of water versus nitrogen limitation in northeastern forests, these results suggest that spatial patterns of NPP for hardwoods and pines can be largely captured using currently available data sets, while substantial uncertainties exist for spruce-fir.

Introduction

Ecosystem scientists have become increasingly interested in the spatial patterns of important ecological processes and the environmental factors that influence them. This interest stems from the recognition that spatial heterogeneity of environmental and ecological variables interact in ways that make site-specific information alone insufficient for understanding natural

systems and coping with the large-scale environmental problems society currently faces.

Several decades of ecosystems research have provided enough information about processes such as photosynthesis, transpiration and decomposition for scientists to build simulation models that predict properties such as biomass production, soil carbon storage and nitrogen cycling rates (e.g., Parton et al. 1988; Raich et al. 1991; Running and Gower 1991; Aber et al. 1997). Along with remote sensing and geographic information systems (GIS), these models can

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be used to extrapolate predictions across larger spatial scales (Burke et al. 1990; Raich et al. 1991; McGuire et al. 1992; Neilson et al. 1995; Vempey 1995). This approach holds great potential for assessing the effects of factors such as air pollution and climate change and also provides a tool for resolving different environmental controls on ecosystem function (e.g., Schimel et al. 1996).

For these goals to be realized, several issues require careful attention. Because ecosystem models (and ecosystems) are very sensitive to the environmental factors that drive them, reliable spatial data sets of important input variables must be obtained from remote or ground-level sources. This can be challenging and often requires making significant assumptions where reliable data are not available. For example, models are often run using potential vegetation where maps of actual vegetation have not been developed. Because human activities have altered the distribution and function of many ecosystems (e.g., Foster 1992), results from these studies may apply to something very different from actual conditions. Where data limitations exist, sensitivity analyses should be performed to test the potential effects of the resulting assumptions. This is a critical, but often overlooked step in ecosystem modeling. Lastly, but of equal importance, model output should be validated at all possible opportunities.

In this paper, we present results from a regional modeling exercise aimed at predicting forest productivity and water balances across the northeastern U.S. using an uncalibrated ecosystem model (PnET-II Aber et al. 1995), a regional climate data set (Ollinger et al. 1995) and a satellite-derived map of current vegetation (Lathrop and Bognar 1994). We also present validation of predicted forest productivity using data from independent field studies, and predicted runoff using data from U.S. Geologic Survey stream gauges. Regional studies are valuable because policy decisions are often made at regional rather than continental or global scales, and because they provide an important intermediate between detailed plot-level information and coarse-scale modeling of global fluxes.

Methods

PnET-II

PnET-II (Aber et al. 1995) is a monthly time step, canopy- to stand-level model that was built on several

generalized relationships. Maximum leaf photosynthetic rate (A_{\max}) is determined as a linear function of foliar nitrogen content, following a strong relationship between the two across species from diverse ecosystems (Field and Mooney 1986; Reich et al. 1995). As such, foliar N serves as a surrogate for site nitrogen availability, assuming that N availability and photosynthetic capacity in foliage are related to N dynamics in soils. Stomatal conductance is related to the actual rate of net photosynthesis, making plant water use efficiency an inverse function of the atmospheric vapor pressure deficit (Sinclair et al. 1984; Baldocchi et al. 1987). This allows transpiration to be predicted from canopy photosynthesis and climate and provides a dynamic link between the carbon and water balance portions of the model.

These relationships are used in the model to construct a multi-layered forest canopy in which available light and specific leaf weight (SLW) decline with canopy depth. Light attenuation is based on the Beer-Lambert exponential decay equation ($y = e^{-k \cdot \text{LAI}}$). Changes in SLW are based on Ellsworth and Reich (1993) producing canopy gradients in area-based, but not mass-based foliar nitrogen concentration. Photosynthesis is calculated in a numerical integration over 50 canopy layers in order to capture the effect of gradual light extinction on total canopy carbon gain. Photosynthetic response curves for light and temperature were derived by Aber and Federer (1992). The photosynthetic response to vapor pressure deficit (VPD) is determined as a power function derived by Aber et al. (1996). Actual evapotranspiration and moisture stress are calculated as functions of plant water demand and available soil water, which is determined using equations from the Brook model (Federer and Lash 1978).

Equations in the model are structured in a series of six subroutines, the first five of which operate in a monthly time step. *AtmEnviron* calculates vapor pressure deficit and cumulative growing degree days, *Psn* determines leaf area display and potential photosynthesis in the absence of drought stress, *WaterBal* calculates available water, drought stress, actual net photosynthesis and runoff, *AllocateMo* calculates tissue respiration and allocation to wood and roots and *SoilResp* calculates CO₂ flux from soils. The final subroutine, *AllocateYr*, allocates accumulated carbon to buds and a wood storage pool for next year's leaf and wood growth.

Regional data base

The northeast study region is the portion of the U.S. north of 41 deg N latitude and east of 76 deg W longitude. It includes the New England states, eastern New York and a portion of northeastern New Jersey and Pennsylvania. Environmental inputs required by PnET-II are monthly averages of maximum and minimum daily temperature, vapor pressure and solar radiation, total monthly precipitation, forest type and plant-available soil water holding capacity (WHC). Climate inputs were generated by a statistical model known as Climcalc, developed for the northeast region from long-term (30 year) climate records (Ollinger et al. 1995). Monthly temperature and precipitation were estimated for each grid cell of a 30 arc sec (approximately 1 km) digital elevation model (DEM) using multiple regression equations based on geographic position and elevation. These equations capture regional and temporal trends in temperature and precipitation, but do not account for local variation such as lake effect precipitation and nighttime valley temperature inversions. Atmospheric vapor pressure was determined as a function of the minimum daily temperature, assuming that nighttime air temperatures decrease only to the point at which dew formation begins. Solar radiation was determined by combining equations for potential radiation with actual radiation measurements made at 11 locations within the study region. Monthly potential radiation was calculated for each grid cell of the DEM using latitude, slope, aspect and time of year. This was then multiplied by the ratio of measured to potential radiation, determined monthly for the 11 measurement stations.

Forest type was determined from a Land Use/Land Cover map (LULC), developed by Lathrop and Bogner (1994) using AVHRR (Advanced Very High Resolution Radiometer) satellite data in combination with existing USGS Land Use/Land Cover data (Figure 1). The map identifies hardwood, spruce fir, mixed hardwood/spruce fir and mixed hardwood/pine forest types as well as a number of non-forest categories at 1 km resolution. Approximately 70% of the region is classified as forest; the remainder is mostly agricultural and urban.

Vegetation-specific input parameters such as foliar nitrogen, specific leaf weight and leaf retention time were determined by Aber et al. (1995) for each forest type using data from field measurements within the region. The nitrogen content of foliage is the most important of these parameters because it determines

the maximum attainable rate of photosynthesis. In the absence of a regional foliar N data layer, we assigned a single value to each forest type identified in the LULC map. After Aber et al. (1995), we used values of 2.2% for hardwoods, 1.2% for pines and 0.8% for spruce-fir. Although variation in foliar N within a forest type is generally small with respect to variation across forest types (Newman et al. 1994; Martin and Aber 1997), these are obviously important generalizations.

A plant-available soil water holding capacity (WHC) map for the northeast region has been derived from the U.S. Soil Conservation Service's STATSGO data base (SCS 1991) by Lathrop et al. (1995). However, comparison of these data with the county-level soil survey data from which they were derived showed poor agreement (Lathrop et al. 1995). The authors attributed this to the high degree of spatial variability exhibited by soils in areas of complex terrain combined with the aggregated nature of the STATSGO-derived data. As an alternative, we used the soil hydrology equations of Clapp and Hornberger (1978) to evaluate plant available water under the range of soil properties typically encountered in northeastern forests. Interestingly, for soils ranging from loamy sands to silty clays, texture had a small effect compared with the effects of rooting depth and the fraction of coarse fragments. Assuming a rooting depth of 1 m and 25% coarse fragments, most well drained till soils produced a plant available water holding capacity of 12 cm. Because of uncertainties surrounding the STATSGO-derived data, we held soil WHC at this value for all model runs.

Regional model runs

For regional analyses, all GIS input data layers were georeferenced and converted to a 30 arc sec grid (approximately 1 km). For each grid cell, geographic coordinates and elevation were read from the DEM and used by Climcalc to calculate maximum and minimum temperature, vapor pressure, precipitation and solar radiation. Vegetation type was read from the AVHRR-derived Land Use/Land Cover map. Grid cells classified as mixed were run twice and the final output value was calculated as a weighted average of the two runs, assuming a ratio of 40:60 for hardwood/spruce-fir and 40:60 for hardwood/pine. These values were determined by comparing the LULC map with USDA Forest Inventory data for growing stock of these forest types (Kingsley 1985). Because high elevation forests experience stresses that are not included in the model (e.g., wind damage), we limited model runs to grid

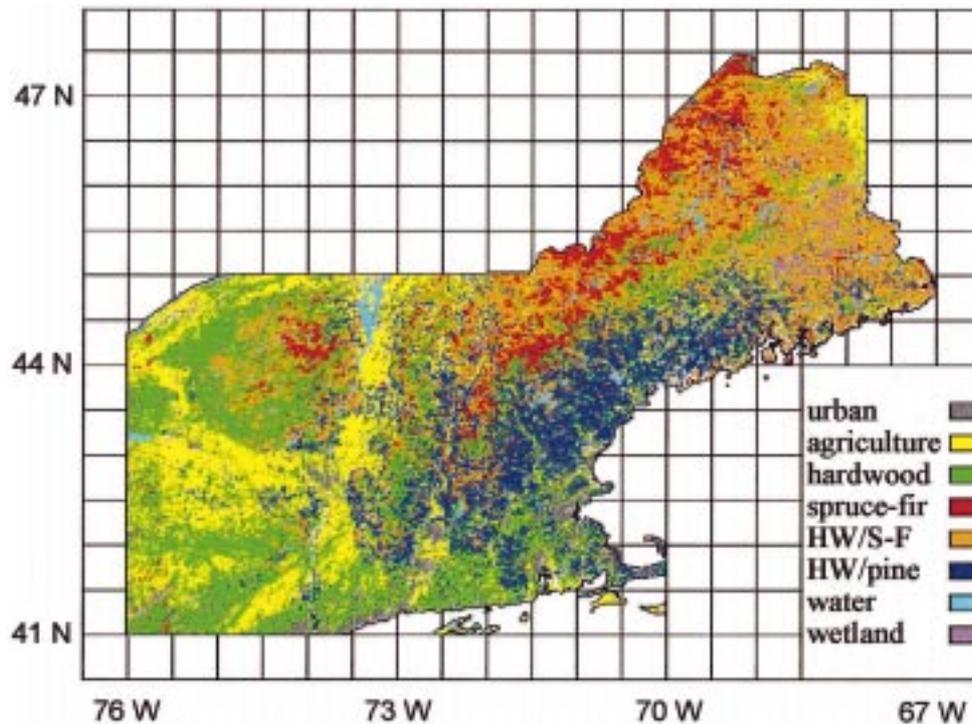


Figure 1. AVHRR-derived Land Use/Land Cover map of the northeast study region. (after Lathrop and Bognar 1994).

cells located below 1200 m, roughly the elevation at which stresses unique to the subalpine zone begin (Reiners and Lang 1979). Elevations above 1200 m represent less than one percent of the total land area of the region.

Sensitivity analysis

Predicted patterns of forest productivity reflect how equations in the model respond to climatic gradients across the region. However, these trends are also dependent on assumptions for soil water holding capacity and foliar nitrogen concentrations. In order to assess the importance of these assumptions, we performed sensitivity analyses using a Monte Carlo approach. This involved conducting multiple model runs where inputs for temperature, precipitation, foliar N and soil WHC were determined stochastically using appropriate distribution functions. For each run, geographic location and elevation were chosen randomly, but were limited for each forest type to the range in which it occurs. For elevation, we used a randomization function that reproduced the skewed distribution of the DEM. This effectively limited variation in climate to values experienced by each forest type within the region. Variation in foliar nitrogen was restricted

to values reported in the literature for northeastern hardwoods and conifers. Those values were: 1.8 to 2.6% for hardwoods, 0.9 to 1.5% for pines and 0.7 to 1.2% for spruce-fir (Newman et al. 1994, Bolster et al. 1996). For soil WHC, we used values ranging from 6 cm, representing a sand with 50% stone content, to 18 cm, representing a clay loam with no stones. For foliar N and WHC, we used a randomization function that produced a normal distribution as described by Hamilton (1989). The model was run a total of 1000 times for each forest type. The relative importance of temperature, precipitation, foliar N and WHC were evaluated by the degree to which each were correlated with predicted NPP.

Validation

There have been relatively few measurements of forest productivity within the study region and at present, there are no data-driven maps with which to test predicted spatial patterns. Nevertheless, comparison of predicted values with existing measurements can still provide insight into the model's performance. Forest productivity (total or aboveground) has been measured for mature pine and hardwood forests at the Harvard Forest in Massachusetts (Magill et al. 1997), for hard-

wood forests at the Bear Brook watershed in Maine (Magill et al. 1996), for hardwood and mixed forests at three elevations in the Hubbard Brook Experimental Forest in New Hampshire (Whittaker et al. 1974), for young pin cherry stands in northcentral New Hampshire (Marks 1974) and for a high-elevation balsam fir stand on Whiteface Mountain, New York (Sprugel 1984). We validated the model for these locations by generating pixel values for the latitude, longitude, elevation and forest type of each site. Specifying the correct forest types removed the regional land cover map as a potential source of error, but allowed a greater number of validation points to be used since several sites included measurements for more than one forest type. Potential sources error come from the model, the climate inputs generated by Climcalc and the parameter values used in the regional model runs. No adjustments were made to any of these for the site-level validation. Predictions were generated for total NPP or aboveground only (ANPP) depending on the data available. Where both were reported (Whittaker et al. 1974), we used ANPP only because fine roots were not measured, but are included in the model and can be an important fraction of belowground production.

Runoff predictions were validated against observations from gauged watersheds within the region that are part of the USGS Hydro-Climatic Data Network (HCDN, Slack and Landwehr 1992) and contain long term (>30 year) streamflow records. We restricted the comparison to watersheds that are at least 90% forested since water balances of nonforested lands can vary considerably from those of forests. We also eliminated watersheds where dams, reservoirs, or other human activities impede natural flow rates. The resulting dataset consisted of 34 watersheds ranging in size from a few to several thousand square kilometers, spread relatively evenly across the region.

Streamflow measurements represent water balances that are spatially-integrated over the entire surface of a watershed. Thus, runoff validation would ideally be conducted by averaging predicted values across all grid cells that lie within a given watershed. At present, this is not possible because the boundaries defining the necessary watersheds are not available in a digital format. As an alternative, we used single pixel values coinciding with the latitude, longitude and mean basin elevation of each watershed as given by HCDN. Model predictions were compared with observed mean annual runoff from the period of 1951–1988 (Slack and Landwehr 1992).

Results and discussion

Model predictions

Predicted annual net primary production ranged from approximately 700 to 1450 g m⁻² yr⁻¹ with a regional mean of 1084 g m⁻² yr⁻¹ (Figure 2a). In general, predictions increased from north to south, following a gradient in temperature and growing season length, although maximum values were attained at mid elevations in the southern Catskill mountains where precipitation was high enough to eliminate mid summer drought. Predictions were highest in areas of pure hardwood due to the higher photosynthetic rates of broad-leaf deciduous species, as compared to coniferous evergreen species. Lowest growth rates occurred in northern and high elevation spruce-fir forests which had the shortest growing season and lowest photosynthetic rates. Intermediate NPP occurred in mixed hardwood/pine forests along the coastal plains of central New England.

Spatial patterns in wood growth followed patterns of NPP, but exhibited a greater range of variation. Predictions ranged from 250 to 900 g m⁻² yr⁻¹ with a regional mean of 550 g m⁻² yr⁻¹ (Figure 2b). PnET-II calculates wood growth as a function of the difference between total biomass production and leaf plus root production after a portion of the remaining carbon is withheld for a reserve pool. The only constraint on wood growth insures that under stressful conditions, the ratio of wood to leaf growth does not fall below a critical level, specified as a parameter in the model (1.5 for hardwoods and 1.25 for conifers, Aber et al. 1995). This serves to prevent foliar production in excess of that which can be supported by new xylem tissue. As such, wood growth is the lowest allocation priority in the model and is least constrained by the model's structure. Hence, it is more sensitive to environmental fluctuations than leaf or root growth.

Predicted annual runoff averaged 63 cm, ranging from approximately 24 cm in the northwest corner of the region to nearly 150 cm at high elevations in the White Mountains of New Hampshire (Figure 2c).

The distributions of predicted NPP and wood production show three distinct peaks (Figure 3a, b), corresponding to areas of hardwood (highest values), mixed hardwood/conifer (intermediate values) and spruce-fir (lowest values). This discontinuous pattern results from the fixed hardwood/conifer composition assigned to mixed pixels in the AVHRR land cover map. In reality, these areas undoubtedly contain a range of

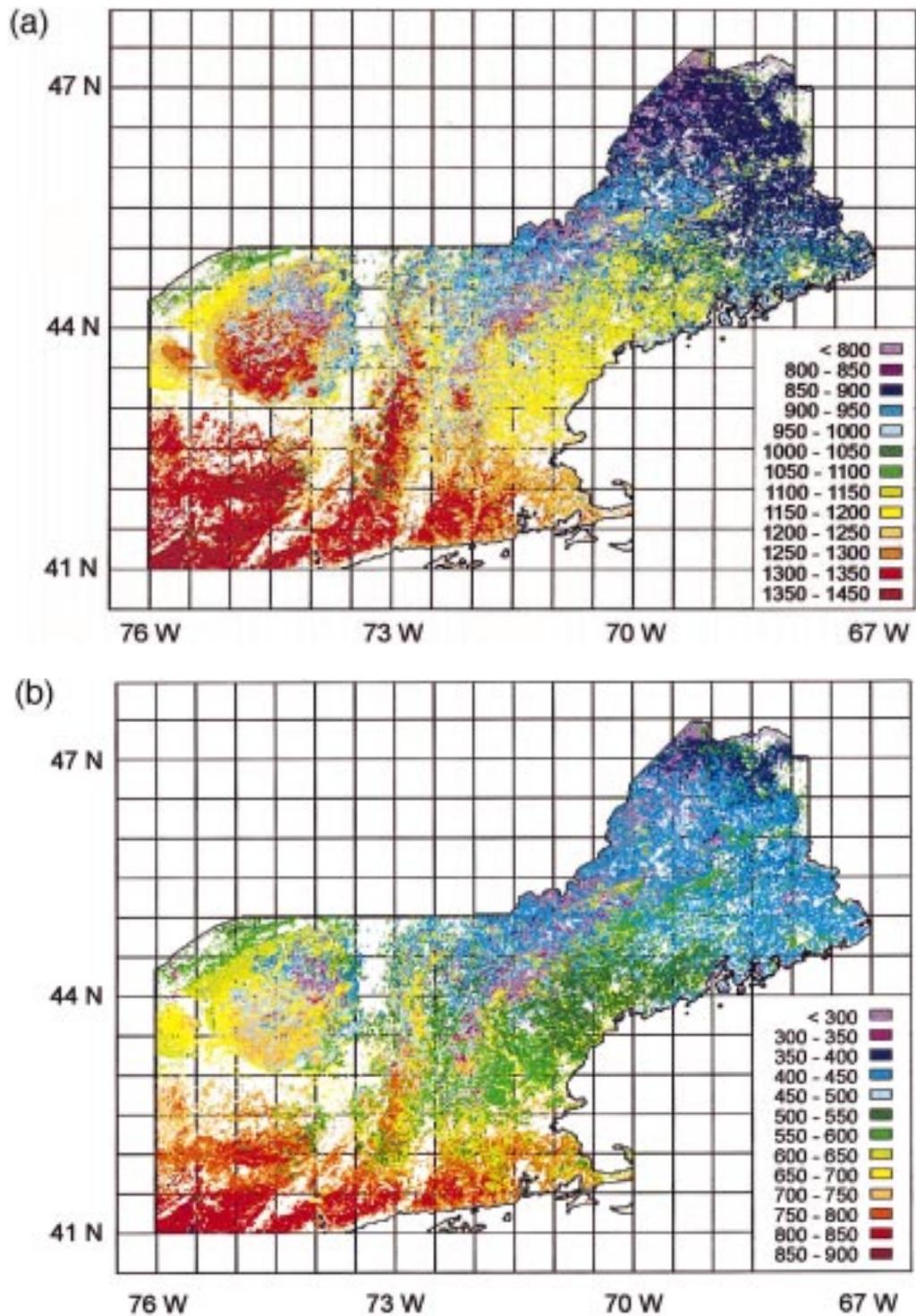


Figure 2a-c. Predicted annual NPP (a), wood production (b), and runoff (c) generated by PnET-II in conjunction with the regional GIS data base. Blank areas are non-forest.

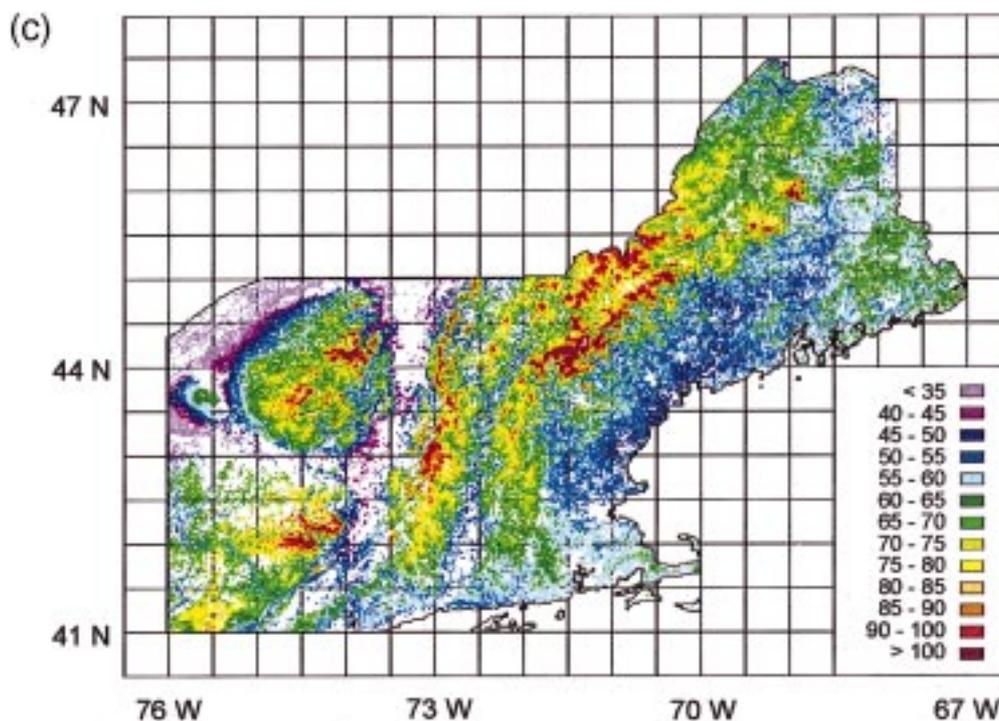


Figure 2. Continued.

hardwood/conifer ratios which would produce a more continuous distribution of values. In contrast, predicted runoff showed a unimodal distribution (Figure 3c). Although potential transpiration is driven by photosynthesis, and is generally higher for hardwood than coniferous forests, this was offset by the longer growing season and higher precipitation interception rate of conifers. Differences that do occur between forest types are masked by the greater importance of variation in precipitation.

Comparison of the spatial patterns of predicted growth with those of input climate variables revealed several interesting trends. In general, predicted growth rates were related to precipitation and annual growing degree days as these variables relate to the availability of water and energy. Between vegetation types, however, distinct differences occurred. For hardwoods, the strongest correlation occurred between NPP and precipitation (Figure 4a) with a much weaker correlation between NPP and growing degree days. This results from the relatively high photosynthetic rates of hardwoods, which drive transpiration and soil water consumption to a point where water limitations occur. For pine, NPP was correlated with both growing degree days and precipitation, but in different parts of its range. In northern areas, the relationship was strongest

with growing degree days because growth rates were low enough that available water supplies were not depleted. Through warmer areas to the south, this trend was replaced by a stronger correlation with precipitation as transpirational demands increasingly depleted available soil water (Figure 4b). For spruce-fir, which has the lowest photosynthetic rate and is restricted to northern and high-elevation areas, the only significant trend was with growing degree days (Figure 4c).

Sensitivity analyses

The relationships in Figure 4 indicate an interaction between model sensitivity to temperature and precipitation, variables for which regional data are available. Results of randomized sensitivity analysis (Table 1) indicate additional interactions with foliar nitrogen and plant-available soil water holding capacity (WHC), variables for which reliable data layers are not currently available at the regional level. As such, these results represent the degree to which the trends in Figures 4a–c depend on assumptions made about these missing data layers.

Within the randomized model runs, the strongest predictors of NPP for hardwood and pine forests were precipitation and soil WHC, indicating that water lim-

Table 1. Sensitivity of predicted NPP to climate, foliar N and soil WHC for each forest type as indicated by correlation coefficients (r^2) from regressions of NPP against each variable alone and in combination. Climate data are summarized as annual precipitation (PPT) and annual growing degree days (GDD). Foliar N (Fol N) is mass-based leaf nitrogen concentration and soil WHC is plant-available soil water at field capacity. $n = 1000$. All variables were significant at $p < 0.05$ except where listed as NS.

	r^2			Std. err.		
	Hardwood	Pine	Spruce-fir	Hardwood	Pine	Spruce-fir
PPT	0.46	0.27	NS	83	92	78
GDD	0.02	0.02	0.10	108	106	74
Fol N	0.16	0.18	0.74	101	100	40
WHC	0.27	0.25	NS	93	93	78
PPT + GDD	0.54	0.32	0.11	81	89	73
Fol N + WHC	0.40	0.38	0.74	83	84	40
ALL	0.90	0.78	0.90	35	51	25

itations were common in both forest types under the range of conditions simulated. The stronger correlation with precipitation than WHC indicates that regional variation in precipitation had a greater effect on available water than did our simulated range of WHC. Spruce-fir NPP showed the opposite trend, being unrelated to water availability and strongly correlated with foliar N. This results from the fact that spruce-fir transpiration rates were rarely high enough to exhaust soil water supplies and induce water stress.

The model's relatively low sensitivity to foliar nitrogen for hardwood forests countered our expectations based on earlier, site-level analyses which showed foliar N to be a critical input parameter for this forest type (Aber et al 1996). These results are not contradictory, but rather demonstrate the influence of scale in determining the relative importance of different ecological processes. Foliar N varies over finer spatial scales than precipitation, and for local areas, appears to control patterns of productivity via its affect on photosynthesis and carbon gain (Martin and Aber 1997). At the broader regional level, however, variation in precipitation overshadowed variation in available N, and water limitation became the dominant factor.

These trends also suggest interactions between water, nitrogen and carbon dynamics that were observed in several previous modeling exercises (Schimel et al. 1996, Aber et al. 1997). Although nitrogen limitations in terrestrial ecosystems often occur locally through both time and space, large scale patterns of productivity are more often related to patterns of temperature and rainfall. Schimel et al. (1996) addressed this

conflict by using the Century model to evaluate the relative importance of water and nitrogen limitations globally. The model predicted that, under steady-state conditions, nitrogen limitations and water limitations become correlated. This was due to the simultaneous control of carbon and nitrogen fluxes by the water budget. Aber et al. (1997), using a version of the PnET model that includes coupled C and N cycles, reached similar conclusions predicting that N cycling rates in the northeastern U.S. were ultimately limited by water or energy, depending on the C fixation efficiencies of different forest types. The paradox of growth limitations by both water and nitrogen was suggested by both authors to be a function of disturbance, whereby periodic perturbations alter rates of C and N cycling which in turn are constantly moving towards – if never achieving – a state of equilibrium with the ultimate controls set by the physical environment.

Overall, the combined influence of precipitation, growing degree days, foliar N and soil WHC explained between 78 and 90% of the variation in predicted NPP within the randomized model runs (Table 1). Table 1 also shows the degree to which predicted NPP is correlated with PPT and GDD together versus foliar N and WHC together. These combinations are presented to provide an indication of the amount of spatial variation in regional NPP which can be explained by factors for which spatial data bases presently exist versus those for which further data development are required. The strong dependence of NPP on precipitation among hardwoods and pines suggests that regional patterns may be at least partly captured by available data, with uncertainty introduced by the absence of WHC and

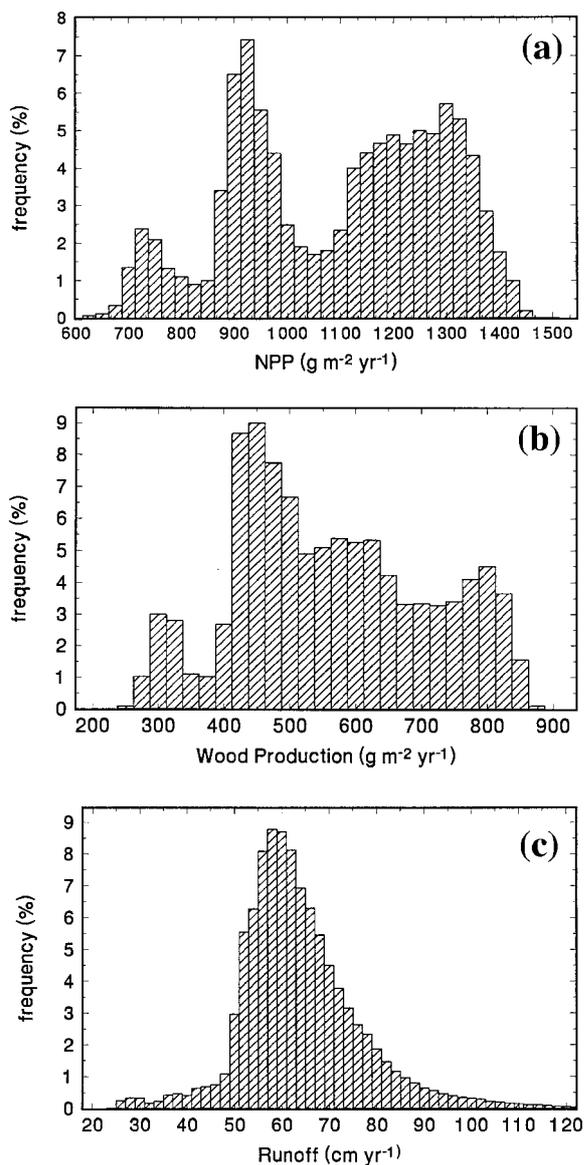


Figure 3. Histograms of predicted annual NPP (a), wood production (b), and runoff (c) showing the distributions of values given in Figure 2. In (c), a small number of data points representing high elevation areas lie off the scale to the right.

foliar N data planes. For spruce-fir, the importance of foliar N raises considerable uncertainties in current predicted spatial patterns across the study region.

Validation

Predicted forest production rates were generally in good agreement with measured values (Table 2). The mean absolute error between predicted and observed values was 12.5%. The two sites with poorest agree-

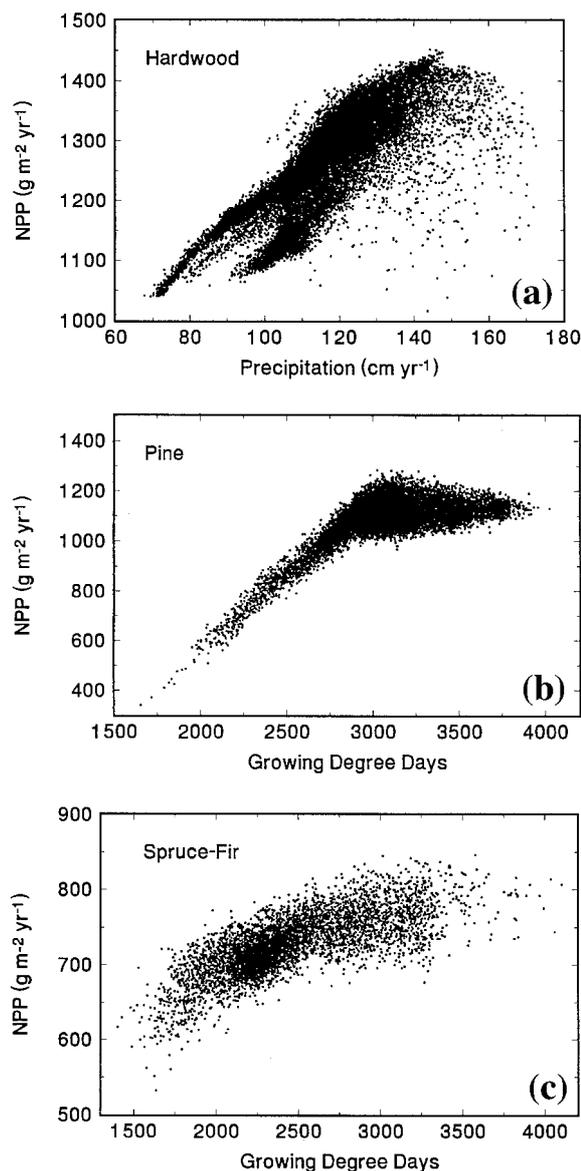


Figure 4. Relationships between predicted NPP and climate for each forest type: (a) hardwood NPP vs annual precipitation, (b) pine NPP vs. annual growing degree days and (c) spruce-fir NPP vs. annual growing degree days. In 6a, data points falling off the relationship to the upper right reflect high elevation areas where temperature limitations become increasingly important.

ment were the high elevation balsam fir stand, where the predicted value was less than half of that measured, and the Harvard Forest hardwood stand, where the model overpredicted by 20%. In both cases, measured values for foliar nitrogen were reported and appear to explain much of the disagreement. Sprugel (1984) measured an average foliar N of 1.59% at Whiteface

Table 2. Predicted and measured biomass production ($\text{g m}^{-2} \text{yr}^{-1}$) for several locations across the northeastern U.S. Abbreviations are: BB = Bear Brook watershed, ME; HF = Harvard Forest, MA; HB = Hubbard Brook, NH (low, mid and high elevations); NNH = Northern NH and WF = Whiteface Mt., NY. ANPP is aboveground net primary production, NPP is total net primary production.

Site	Variable measured	Forest type	PnET-II	Observed	Source
BB	ANPP	HW	909	893	Magill et al. 1997
HF	ANPP	HW	1010	843	Magill et al. 1996
HF	ANPP	Pine	795	757	Magill et al. 1996
WF	ANPP	Balsam fir	456	960	Sprugel 1984
HB low	ANPP	HW	1032	1094	Whittaker et al. 1974
HB mid	ANPP	HW	1013	1010	Whittaker et al. 1974
HB high	ANPP	HW-SF	876	751	Whittaker et al. 1974
NNH	NPP	Pin Cherry	1295	1264	Marks 1974

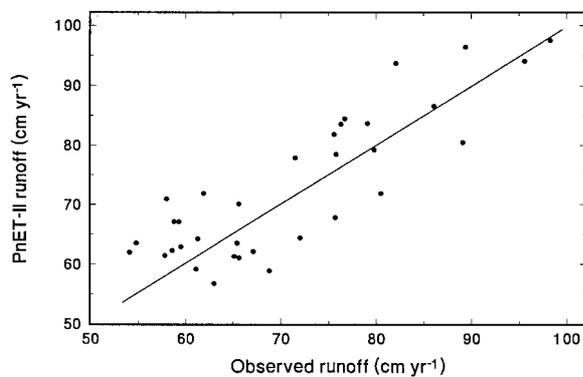


Figure 5. Predicted versus observed runoff for gauged watersheds across the study region with >90% forest cover and no barriers to natural flow rates (dams, reservoirs, etc.). $n = 34$.

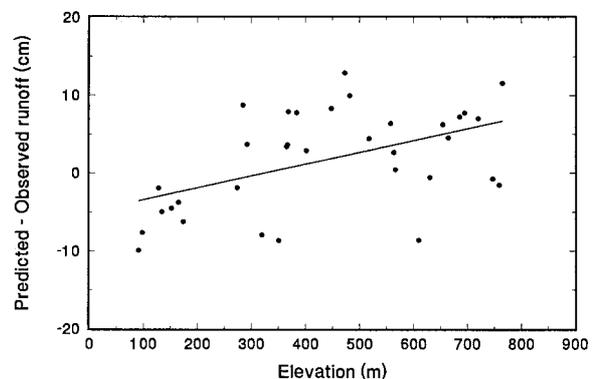


Figure 6. Differences between predicted and observed runoff (Figure 5) in relation to the mean basin elevation.

Mountain, which is high relative to other values reported for balsam fir (Newman et al. 1994; Bolster et al. 1996) and almost twice that used for spruce-fir forests in this study. At Harvard Forest, Magill et al. (1997) reported a foliar N of 1.9% for the hardwood stand, which is low for this forest type and lower than the value of 2.2% used in the model. Using the measured foliar N values resulted in considerably closer agreement for both Whiteface and Harvard Forest (predicted ANPP = 980 and 905, respectively) and reduced the average absolute error to only 5.2% for all validation sites combined.

Predicted runoff was in good agreement with measured values for forested watersheds in the USGS Hydro-Climatic Data Network (Figure 5). Mean annual runoff among the HCDN watersheds was 71.1 cm, compared with the mean predicted value

of 72.6 cm. Regression of predicted against observed values produced an r^2 of 0.73, a standard error of 6.0 cm (8.4%), and a slope and intercept not significantly different from 1 and 0, respectively. Although this indicates generally good spatial agreement across the region, residuals indicated a slight elevation bias whereby the model tended to overpredict runoff at higher elevations and underpredict at lower elevations (Figure 6). At present, it is unclear whether this bias results from the elevation coefficients used to estimate precipitation, the model's calculation of canopy transpiration, the use of a fixed water holding capacity or the use of single pixel values for each watershed (as opposed to extracting predictions from the entire surface of each watershed). Although any of these may have caused the observed bias, the precipitation-elevation coefficients used by Climcalc are perhaps

most suspect because they were derived from relatively few high elevation weather stations. Additional efforts aimed at resolving this issue should lead to improvements in future runoff predictions.

Conclusions

This analysis provided regional estimates of forest production and water yield for the northeastern U.S. using a satellite-derived map of current vegetation and an uncalibrated model of forest carbon and water balances. Several interesting trends between forest production and regional gradients in climate were suggested. Among hardwood forests, NPP was strongly correlated with precipitation suggesting water limitation as an important factor controlling regional patterns of productivity. NPP within pine forests was correlated with precipitation across much of the region, except in northern and upper elevation areas where transpirational demands are low. In these areas, stronger relationships were observed between NPP and annual growing degree days. Among spruce-fir forests, which are found only in northern and high elevation areas, NPP was rarely limited by water and was most strongly related to growing degree days.

Randomized sensitivity analyses showed that model sensitivity to inputs for soil water holding capacity (WHC) and foliar nitrogen varied between forest types. Under the range of temperature, precipitation, foliar N and WHC values expected across the region, precipitation was the strongest predictor of NPP among hardwoods and pines, followed by WHC and foliar N. Within spruce-fir forests, water limitations were absent and predicted growth was related only to foliar N. Further research will be needed to determine the actual importance of nitrogen versus water limitation on spatial patterns of productivity.

Model validation showed good agreement between predicted and measured forest productivity and runoff at a number of sites across the region. Differences between predicted and measured forest productivity at two sites were related to data inputs for foliar nitrogen. Differences between predicted and observed runoff were positively correlated with elevation, suggesting an elevational bias in inputs for water availability (precipitation or soil water holding capacity) or processes simulated by the model (e.g. transpiration). Because water and nitrogen are the two most important factors limiting northeastern forest productivity, future efforts

should be directed towards obtaining or improving high-resolution data planes for these variables.

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