Importance of Foliar Nitrogen Concentration to Predict Forest Productivity in the Mid-Atlantic Region

Yude Pan, John Hom, Jennifer Jenkins, and Richard Birdsey

ABSTRACT. To assess what difference it might make to include spatially defined estimates of foliar nitrogen in the regional application of a forest ecosystem model (PnET-II), we composed model predictions of wood production from extensive ground-based forest inventory analysis data across the Mid-Atlantic region. Spatial variation in foliar N concentration was assigned based on a correlation with mean July temperature for deciduous forests and with latitude for coniferous forests. Although the slight variation observed in foliar N in conifers had little effect on predicted wood production, large differences in N concentration in deciduous trees increased agreement with field surveys by 12–59% in individual states and by 17% across the region. The validation revealed the need to develop regional foliar N concentration equations that represent the spatial variations of N concentration in deciduous forests to improve PnET-II's predictions. FOR. SCI. 50(3):279–289.

Key Words: Wood production, forest inventory and analysis data (FIA), validation, ecosystem model, PnET-II.

CARBON AND NITROGEN CYCLES are coupled closely in forest ecosystems. Nitrogen exerts control over the rates of several carbon cycling processes, including net primary production (NPP) (McGuire et al. 1995). Nitrogen is a major constituent of chlorophyll and is involved in carboxylation of enzymes and the reactions of photosynthesis (Waring and Schlesinger 1985). Observed differences in nitrogen concentration of foliage tissue generally reflects changes in enzyme concentration (McGuire et al. 1995). The maximum net photosynthesis rate is often closely related to foliar N concentration (Field and Mooney 1986, Evens 1989). Such a relationship is used widely to conceptualize growth models (e.g., GAP model, Shugart and West 1980) and large-scale carbon models that do not incorporate full N cycling (e.g., DOLY, Woodward et al. 1995; IBIS, Foley et al. 1996; PnET-II, Aber and Federer 1992).

Foliar N concentration is related to many variables, including soil N mineralization and nitrification, soil C:N ratios, species, temperature, and irradiance (Ollinger et al. 2002, MaGill et al. 1996, Yin 1992, 1993, and 1994, Field 1983, Pastor et al. 1984, Chen et al. 1993) and also may be affected by other factors: land-use history, changes in CO_2 concentration, acid deposition, and limitation of other nutrient element supply (Aber and Driscoll 1997, Goodale and Aber 2001, Woodward et al. 1991, Hallett and Hornbeck 1997). Species traits, N availability, and climate are three control factors that likely determine canopy foliar N concentration and cause the formation of complex variations in foliar N concentration at broad spatial scales.

Yude Pan, Research Forester, USDA Forest Service, Global Change Research, Newtown Square Corporate Campus, 11 Campus Blvd., Suite, Newtown Square, PA 19073—Phone: (610) 557-4205; Fax: (610) 557-4200; E-mail: ypan@fs.fed.us. John Hom, Deputy Program Manager, USDA Forest Service, Newtown Square Corporate Campus, Newtown Square, PA 19073. Jennifer Jenkins, Visiting Assistant Professor, Gund Institute for Ecological Economics, University of Vermont, Burlington, VT 05402. Richard Birdsley, Program Manager, USDA Forest Service, Newtown Square Corporate Campus, Newtown Square, PA 19073.

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Field data of foliar N concentration are relatively rare and often measured for specific species and study sites. Remote sensing data from NASA's Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) are used to determine forest canopy chemistry spatially (MaGill et al. 1996). The spatial resolution for calibrating canopy-level chemistry (e.g., nitrogen concentration, lignin, and cellulose) can be as fine as 20 m (Martin and Aber 1997). It is promising that the data of the remote-sensing AVIRIS provides useful information of canopy N concentration to drive spatially referenced ecosystem models. The shortcoming of using the AVIRIS information is that it needs great computer capacity. The selected first-difference reflection bands of AVIRIS data using stepwise regression for calibrating canopy chemistry cannot avoid arbitrariness completely and are specified for the study sites where calibration data are collected. Uncertainties associated with the AVIRIS data correction process, calibration, and sampled filed data could be remarkable in the remote-sensing-based predictions of canopy chemistry. Because of these limits, the method seems applicable to fine-resolution and local-scale studies that usually cover a few hundred square kilometers. The canopy nitrogen data at regional or continent scales seem unable to rely completely on the remote-sensing-based technology.

Although some mathematical models estimate foliar N concentration (e.g., Smith and Martin 2001, Ollinger et al. 2002, Woodward et al. 1995), none is accepted for characterizing canopy foliar N concentration, especially across a broad landscape. Process-based carbon models in ecosystem studies and global change research often must assume constant values of foliar N concentration but would improve in accuracy if spatially explicit data on N status were available. The effect on the model predictions using spatial N concentration data as constants is explored in this article.

In this study, we use the PnET-II model to predict forest production in the Mid-Atlantic region with different foliar N concentration. The PnET-II is a process-based forest ecosystem model that uses spatially referenced climate, vegetation, and soil water holding capacity data to estimate carbon and water fluxes in forest ecosystems monthly (Aber and Federer 1992, Aber et al. 1993, 1995). Foliar N concentration is an important parameter in the PnET-II model because it defines maximum photosynthesis by a linear algorithm. Because spatial data of foliar N concentration are limited, constant foliar N concentrations are assumed respectively for deciduous and coniferous forests (Aber et al. 1993, 1995). The alternative canopy N concentration data used in this study are spatially referenced and generated using equations developed by Yin (1993) that reflect the effects of climate gradients on canopy nitrogen concentration.

To examine how the equation-generated spatial foliar N concentration compared with constant foliar N concentration, we compare model predictions of forest wood NPP with wood productivity derived from ground-based forest inventory and analysis data (Jenkins et al. 2001). Although model validation is a critical step, it is a challenge when faced with highly variable natural landscapes.

Methodology and Data

The PnET-II Model

The PnET-II model is a simple process-based ecosystem model that calculates monthly carbon gain and water balance in forest ecosystems. It is used to estimate NPP, wood production, and water yield in forest ecosystems for contemporary climates and projected climate scenarios at both stand and regional levels (Aber and Federer 1992, Aber et al. 1993, 1995). The model is well-validated for NPP and water yield predictions at locations within the northeastern United States (Ollinger et al. 1998).

Daily gross photosynthesis per unit leaf area and total canopy gross photosynthesis in PnET-II are expressed as:

$$\mathrm{GrossPsn} = \mathrm{GrossPsn_{max}} \times \mathrm{DTemp} \times \mathrm{Dwater} \times \mathrm{DVPD} \quad (1a)$$

$$\mathrm{CanopyGrossPsn} = \sum_{i=1\ (\mathrm{top})}^{50} \mathrm{Grosspsn} \times \mathrm{LightEff_i} \times \mathrm{FolMass_i} \quad (1b)$$

where $\mathrm{GrossPsn_{max}}$ is a function of daily maximum gross photosynthesis (μmol $\mathrm{CO_2 \cdot m^{-2}}$ leaf $\mathrm{area \cdot s^{-1}}$); Dtemp, Dwater, and DVPD are the scalar functions between 0 and 1 for expressing the effects of temperature, water availability, and vapor pressure deficit. In Eq. 1b, the function $\mathrm{LightEff_i}$ varies between 0 and 1 and represents the light effect on photosynthesis at canopy layer i; $\mathrm{FolMass_i}$ ($\mathrm{g\ m^{-2}}$) is foliage biomass at layer i.

In the model, maximum net photosynthesis, $\mathrm{NetPsn_{max}}$ (i.e., the difference between maximum gross photosynthesis $\mathrm{GrossPsn_{max}}$ and leaf respiration) is a linear function of foliage N concentration (Aber and Federer 1992) and expressed as:

$$\mathrm{NetPsn_{max}} = \mathrm{Amax} + \mathrm{Bmax} \times \mathrm{N\%} \quad (2)$$

where Amax and Bmax are parameters for the linear relationship between foliage N concentration and maximum net photosynthesis. Both are higher for deciduous than coniferous forests. The parameters were derived from field studies for the northeast region of America (Aber et al. 1995). Many studies indicated that foliar N concentration may change with canopy structure (Waring and Schlesinger 1985). Although the canopy in the model was divided to 50 layers to incorporate effects of light attenuation on photosynthesis, there were no available foliar N concentration data representing variations over the canopy to refine the calculation of the maximum net photosynthesis. In Eq. 2, N% is the percentage of nitrogen in foliage (dry weight). Based on their studies, we assigned a default value of 2.2% for deciduous forests and 1.1% for coniferous forests (Aber and Federer 1992).

Net carbon canopy gain in the model was accumulated based on the net canopy photosynthesis minus plant growth and maintenance respiration. The carbon allocation routine in the model then accumulates carbon canopy gain over a year and allocates the product to pools of leaf, root, and wood based on leaf area and relationship between aboveground litter production and carbon allocation to roots (Aber and Federer 1992, Raich and Nadelhoffer 1989).

Model Inputs

Vegetation, monthly minimum and maximum temperature, monthly precipitation, monthly solar radiation data sets, and soil water holding capacity information were required to run the model. The spatial resolution of the model simulation was 30 arc-seconds (approximately 1 km). Each data set included 705,600 pixels that covered the Mid-Atlantic region between 36°30′ and 43°30′ N, 74° and 81° W.

Forest types were derived from the map of USDA Forest Service AVHRR Forest Type Groups of the United States (Zhu and Evans 1994). The map identified forest types at a 1-km resolution. The forest types in the original data set were recategorized to match the plant functional types used in PnET-II: deciduous forest, spruce-fir, mixed hardwood with spruce-fir, pine, mixed hardwood with pine. Oak-hickory is the dominant deciduous forest type in the region. Spruce-fir forests are in high mountainous areas of West Virginia and New York. Pine forests include white-red-jack pine types in the northern part of the region, loblolly pine types in the coastal area and the southern area. Mixed hardwood/pine forests represent oak-pine types in this region.

We calculated monthly minimum and maximum temperature for each grid cell from regression equations. Temperature data were 30-year means from 1961 to 1990 derived by the National Climate Data Center (NCDC) database (www.ncdc.noaa.gov/oa/climate/stationlocator.html) from 377 weather stations in the Mid-Atlantic region. Multiple linear regression equations between the monthly minimum/maximum temperatures and latitudes, longitudes, and elevations were developed. The R^2 values for regression analysis indicate that geological locations and elevations explain between 67 and 97% of spatial variations in temperatures. Then we applied regression equations to estimate temperature variables for each grid cell based on its longitude, latitude, and elevation. We derived and aggregated elevation data from United States Geological Survey (USGS) digital elevation model (DEM) at 6″ resolution (USGS 1987).

The monthly precipitation data set was developed by Grimm and Lynch (1997) at 6″ resolution (≈0.2 km). They developed the precipitation data set as a step to estimate wet N deposition for the northeastern United States. The precipitation distribution pattern is greatly influenced by large water bodies and topographical features. The data were developed with a moving neighborhood, weighted linear least squares regression algorithm that estimated precipitation as a function of latitude, longitude, elevation, slope, and topographic aspect. The data were aggregated to 30″ resolution.

We determined monthly solar radiation by combining equations for potential radiation with actual radiation measurements. We calculated monthly potential solar radiation based on the trigonometric algorithm given by Swift (1976) that was a function of latitude, slope, and aspect. We obtained ratios of measured to potential solar radiation in each month, expressed as percentages of sunshine duration, from 15 measurement stations in the region (NCDC www.ncdc.noaa.gov/oa/climate/surfaceinventories.html). The ratios were monthly averages of the measurements and were used to multiply the monthly potential solar radiation to estimate monthly solar radiation. We then extrapolated monthly to the region, using latitude, slope, and aspect data derived from the digital elevation model data (USGS 1987). In the PnET-II model, the radiation at the top of canopy (photosynthetically active radiation) defined light attenuation. Photosynthetically active radiation was calculated as the solar radiation of daylight in $J{\cdot}m^{-2}{\cdot}s^{-1}$.

We derived soil water holding capacity data set at a 1-km resolution from Kern (1994, 1995) and the Natural Resources Conservation Service National Soil database (STATSGO, water.usgs.gov/GIS/metadata/usgswrd/ussoil.html). The data sets were based on a statistical framework with a large sample size derived from the database of the National Resource Inventory. We estimated the soil water holding capacity based on soil texture, soil organic matter, the bulk density and rock fragment, as well as soil depths (Kern 1994, 1995). We adjusted the data to 30″ resolution.

The Constant and Spatial Data of Forest Foliage N Concentration

As discussed earlier, PnET-II uses constant foliar N concentration as a parameter in the model (2.2% for deciduous and 1.1% for coniferous forests). These estimates were considered representative of the foliar N concentrations in northeastern forests (Aber and Federer 1992). They are used also as initial values of foliar N concentration in the PnET-CN version that has a full N cycling subroutine. Although the foliar N concentration in the PnET-CN version changes dynamically, it varies around the initial values within a small range (Pan et al. 2001).

We generated the spatial foliar N concentration data across the study region (Figure 1) using the equations developed by Yin (1993). A series of papers (Yin 1992, 1993, 1994) associated with a large project on atmospheric acid sulfate-nitrate loading explored patterns of foliar N concentration, N availability, and N use efficiency regarding forest type across climatic gradients in North America. These papers revealed important controls of climate gradients on foliar N concentration and related mechanisms that regulate N uptake, foliage growth, and available N supply. Foliage N concentration in forests across North America can be predicted using a single variable related to geographical gradients (Yin 1992, 1993). The best predictor of foliage N concentration for deciduous forests is mean July temperature and latitude for coniferous forests (Yin 1993). Both equations explain 69% of variations and are as follows:

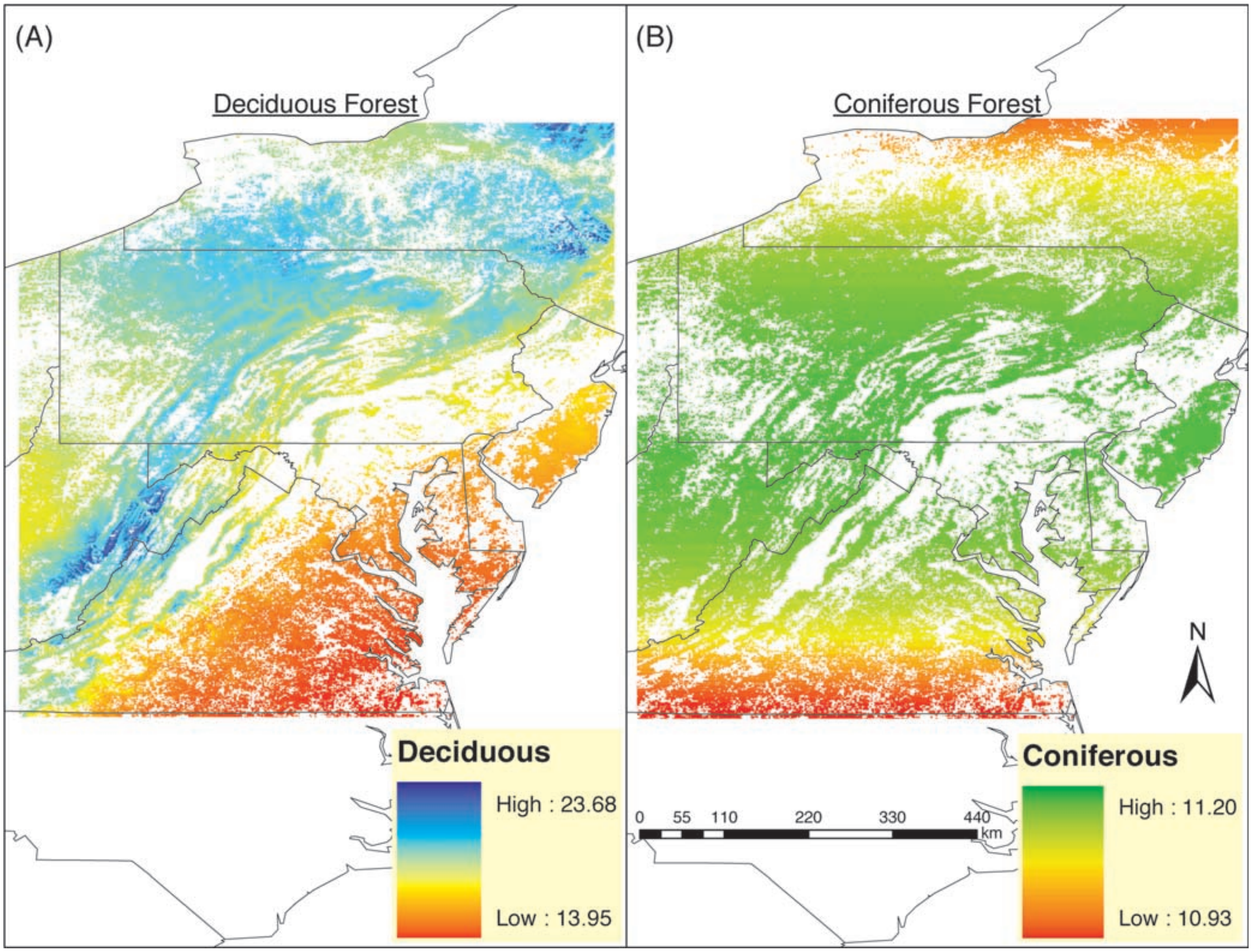

Figure 1. Spatial foliar N concentration (mg g^{-1}) distribution. (A) Deciduous forests; (B) Coniferous forests.

$$N_{dec} = 36.3 - 6.0 \exp(x_1/20) \quad R^2 = 0.69, n = 49 \tag{3}$$

$$N_{con} = 11.2 - 2.4 (x_2 - 40)^2/x_2^{1.3} \quad R^2 = 0.69, n = 58 \tag{4}$$

where N_{dec} is the foliar N concentration for deciduous forests and N_{con} for coniferous forests, x_1 is the mean July air temperature, and x_2 is latitude. However, using the equation-generated foliar N concentration data for the ecosystem models represents only foliar N concentration trends across geographical (climate) gradients and does not represent local factors such as topographical features that may cause smaller-scale variations. We employed the above equations with mean July temperature and latitudes to estimate the concentration of foliar N for both deciduous and coniferous forests in each 30-arc-second grid cell (Figure 1). We then parameterized the PnET-II model, using a constant foliar N concentration value and a spatial foliar N concentration data set, to calculate total NPP and wood NPP.

Forest Inventory and Analysis (FIA) Data and Validation

We used the USDA Forest Service's FIA data to validate the predicted wood production in the Mid-Atlantic region. Since 1928, USDA Forest Service has conducted forest inventories that focused on volume estimation (Birdsey and Schreuder 1992, Wharton et al. 1997, Jenkins et al. 2001). FIA data are recognized as valuable information for validating predictions of large-scale ecosystem models because they are based on statistically designed samples that cover broad forest areas and provide true ground-based values for estimating forest biomass and productivity across heterogeneous regions (Birdsey 1992). Thus, methods to estimate forest biomass and annual primary production based on FIA measurements to validate ecosystem modeling have been developed (Wharton et al. 1997, Jenkins et al. 2001).

The FIA data for validation in this study were derived from FIA plots that have no evidence of damage by insects, logging, diseases, or fire between the two most recent inventories, covering approximately 10–14 years (Jenkins et al. 2001). We estimated complete tree wood biomass (including growing stock, branch, twigs, stump, and woody roots) in two consecutive inventories for different tree species based on those inventory measurements. We multiplied tree-level estimates by expansion factors (i.e., the number of trees per unit area) and derived plot-level estimates at per unit areas basis. We then aggregated and averaged the estimate to the state level for different tree groups. For comparison, we aggregated and averaged the model predictions from grid cells for different tree groups and different states.

Results and Discussion

Spatial Pattern of Foliar N Concentration

A linear algorithm between the maximum photosynthesis and foliar N concentration was developed in the PnET-II model using field data from major broad-leaf species of eastern North American forests (Aber and Federer 1992). Therefore, using spatial data of foliar N concentration instead of constant foliar values would likely affect the model prediction of forest productivity. Figure 1 demonstrates spatial distributions of foliar N concentration for deciduous and coniferous forests across the region, simulated by the foliar N concentration equations (Yin 1993). Foliar N concentration in conifer forests across the region vary slightly and are close to the constant for this type (1.09–1.12% versus constant 1.10%). However, foliar N concentration with deciduous forests has greater variations from the constant (1.39–2.36% versus constant 2.20%, Figure 1). In addition, the spatial distribution of foliar N concentration reflects only the trend in change across a large landscape. Approximately 30% of variations that may relate to other environmental factors were missed in these large spatial patterns. Yin (1993) found that higher foliar N concentration for deciduous trees occurs in colder areas (Figure 1A), which may be a response to slower growth rates and less dilution of available N or an adaptation required for cold hardiness. The highest foliar N concentration for coniferous forests occurs at an approximate latitude of 40° N (Figure 1B) with decreased concentration observed both to the north and south. Nitrogen concentration in foliage was reduced across landscapes from southern and central Europe to northern countries (Meir et al. 2002). Southern and central Europe is at a latitude of 40° N and dominated by conifers; the relationship appears to be consistent with the pattern of N concentration in foliage of coniferous forests in Northern America, which decreases from the mid-latitudes toward northern latitudes.

Effects of Foliage N Concentration on Productivity

We predicted 7% higher NPP at the regional scale (Figure 2) using the constant foliage N rather than spatially variable foliage N in PnET-II (Table 1). However, the model predicted 17% higher wood production (wood NPP) using the constant, indicating that wood production is more sensitive to changes in foliage N concentration than total NPP, probably because of the low priority for wood in allocating carbon product (Fritts 1976). Deciduous forests,

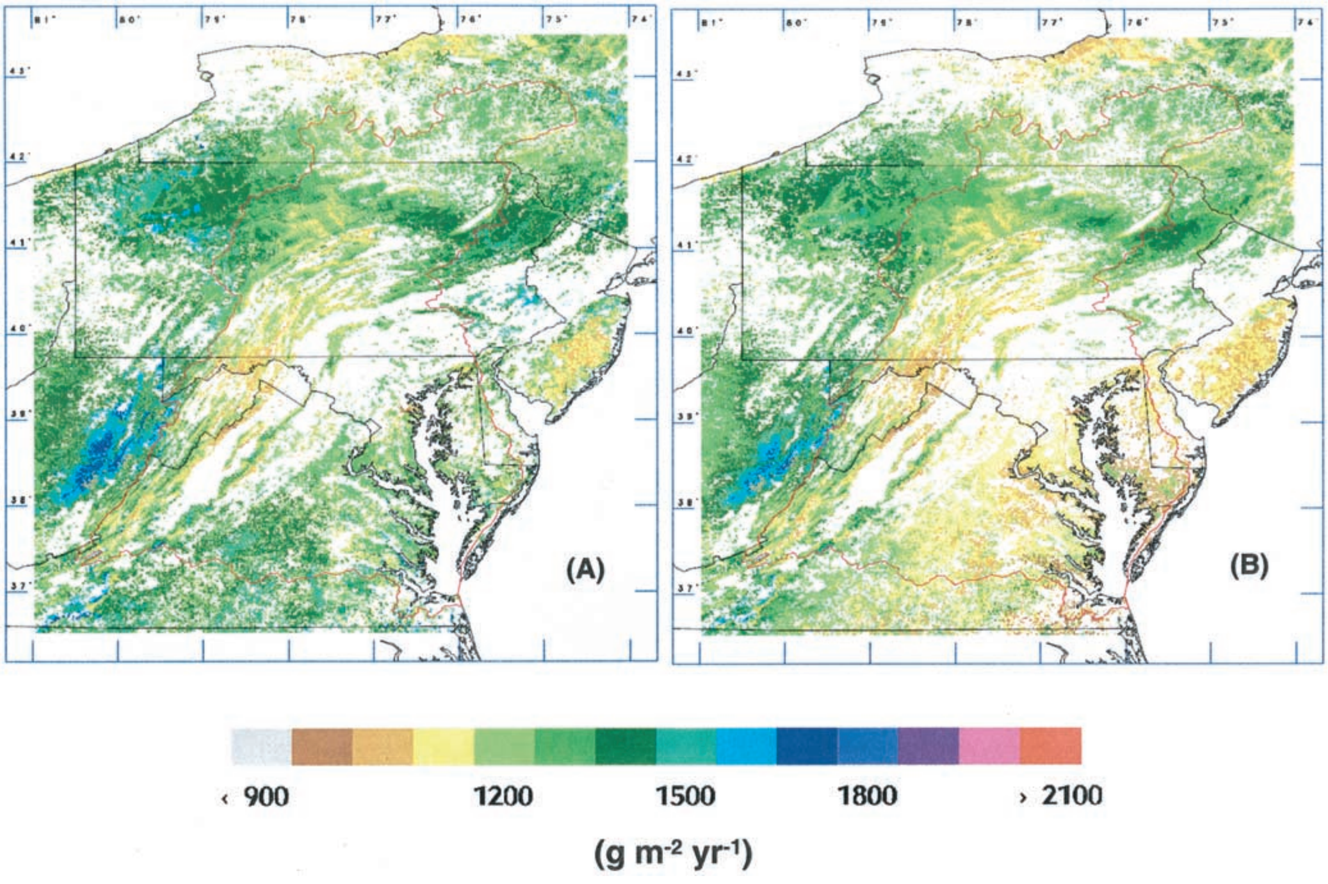

Figure 2. The predictions of NPP by PnET-II (A) with the constant foliage N parameters; (B) with equation-generated spatial foliar N concentration data.

Table 1. The predictions of NPP and wood production by the PnET-II model for the Mid-Atlantic Region.

Model input/parameters	Tree groups*	NGRID (30″)	Total (Tg)	Total NPP (g m^{-2} yr^{-1}) Min	Max	Mean	STD
RUN 1	HW	270,547	245.05	840	1,946	1,385	125.6
Constant	SF	674	0.44	834	1,112	990	67.3
foliar N	HW/SF	4,840	3.77	946	1,337	1,153	51.1
concentration	HW/Pine	29,787	26.44	850	1,889	1,326	134.4
	Pine	29,159	24.18	913	1,820	1,236	100.1
	Region	335,007	299.89	834	1,946	1,363	134.6
RUN 2	HW	270,547	228.45	824	1,770	1,292	131.2
Spatial	SF	674	0.44	834	1,112	990	67.3
foliar N	HW/SF	4,840	3.18	881	1,098	973	36.1
concentration data	HW/Pine	29,787	23.84	856	1,744	1,197	97.2
generated by	Pine	29,159	24.22	920	1,819	1,237	99.8
equations	Region	335,007	280.13	824	1,819	1,274	134.3
				Wood NPP (g m^{-2} yr^{-1}) Min	Max	Mean	STD
RUN 1	HW	270,547	146.28	432	1,402	826	118.1
	SF	674	0.22	355	605	484	62.0
	HW/SF	4,840	2.39	569	906	730	54.7
	HW/Pine	29,787	13.76	383	1,127	689	111.0
	Pine	29,159	8.38	316	752	428	35.6
	Region	335,007	171.03	316	1,402	777	161.6
RUN 2	HW	270,547	125.26	424	1,145	709	107.9
	SF	674	0.22	355	605	484	62.0
	HW/SF	4,840	1.78	504	617	544	13.8
	HW/Pine	29,787	10.83	386	919	544	62.5
	Pine	29,159	8.39	318	749	429	35.4
	Region	335,007	146.48	318	1,145	668	133.6

* HW: oak-hickory, maple-beech-birch, elm-ash-cottonwood, aspen-birch; SF: spruce-fir; HW/pine: oak-pine; Pine: white-red-jack pine, loblolly-shortleaf pine.

which dominate the region, contributed most to the difference in the predicted wood production with the variable foliar N concentrations. Almost no difference existed in either total NPP or wood NPP predictions for coniferous forests with alternative foliar N concentration inputs because with the small change in latitude in this study, foliar N concentration is insensitive to the geographical gradient presented in Eq. 4.

We performed several test runs with PnET-II using different constant foliage N concentrations for deciduous forests and found that when the foliar N concentration is reduced by 0.5%, wood production decreases 21.4–29.6% (Table 2). When foliar N concentration is lower, wood production is more sensitive to the parameters (i.e., with 0.1% less of foliar N concentration from 1.8 to 1.7%) and wood production decreases by 7.1–12.1%. A sensitivity analysis based on the state level shows that the correlation between the change in wood production and the change in foliar N concentration is significant ($R^2 = 0.79$, $P < 0.05$, $n = 15$). This analysis reveals that deciduous wood production is sensitive to foliar N concentration.

The predicted NPP with the spatially variable foliar N concentration data reflects the temperature-controlled pattern (Figure 2B). In contrast, with constant foliar N concentrations, predicted NPP is highly sensitive to precipitation when water is limited and temperature controlled when water supply is sufficient (Figure 2A). Annual NPP predicted with the spatially variable foliar N concentration matches the pattern of foliar N concentration distribution (Figure 2A versus Figure 1A). Summer temperature is lower

Table 2. Wood production estimated by PnET-II with different constants of foliage N concentration (FN).

Tree group	State	Grid no.	PnET estimated NPP (g m^{-2} yr^{-1}) FN = 2.2%	FN = 1.8%	FN = 1.7%	–ΔNPP% –0.4% FN	–ΔNPP% –0.5% FN	–ΔNPP% –0.1% FN
HW	NY	59,062	754.8	608.3	554.7	19.4	26.5	8.8
	PA	107,264	811.5	649.5	591.5	19.9	27.1	8.9
	NJ	7,239	870.7	692.3	617.2	20.4	29.1	10.8
	VA	46,410	878.2	743.3	690.1	15.3	21.4	7.1
	WV	38,616	889.8	712.9	626.3	19.8	29.6	12.1

Table 3. Comparison of forest wood production between the FIA estimates and the PnET-II predictions.

Tree group	State	Plot no.	FIA estimated NPP (g m^{-2} yr^{-1})			
			Min	Max	Mean	STD
HW	NY	741	125	1,267	513	124.6
	PA	761	290	1,108	545	119.2
	NJ	32	296	698	499	110.4
	MD	104	340	1,137	587	128.6
	DE	26	363	1,182	534	158.3
	VA	57	264	1,065	562	172.0
	WV	465	303	1,044	548	122.1
SF	NY	39	173	618	379	100.3
HW/Pine	NY	35	287	654	458	108.3
	PA	18	332	669	462	74.2
	MD	26	335	712	479	100.9
	VA	7	337	750	585	149.0
	WV	14	266	697	425	125.9
Pine	NY	135	267	846	464	109.6
	PA	46	253	812	469	106.7
	NJ	6	221	535	299	118.2
	MD	23	220	580	384	105.5
	DE	7	173	530	390	112.2
	VA	46	117	1,045	515	194.7
	WV	18	203	627	409	109.6

	State	Grid no.	Wood NPP (g m^{-2} yr^{-1}, constant N)				Δ% in mean (vs. FIA)
			Min	Max	Mean	STD	
HW	NY	59,062	432	1,215	755	90.5	+47.2
	PA	107,264	503	1,156	812	95.8	+48.8
	NJ	7,239	661	1199	871	82.7	+74.5
	MD	8,182	547	1,162	885	90.6	+50.8
	DE	1,781	740	978	886	50.7	+66.0
	VA	46,410	454	1,402	878	132.4	+56.4
	WV	38,616	466	1,240	889	129.5	+62.4
SF	NY	208	355	441	398	17.2	+5.0
HW/Pine	NY	1,504	485	873	644	54.5	+40.5
	PA	7,988	433	846	613	72.2	+32.5
	MD	1,442	509	860	681	67.4	+42.3
	VA	17,806	383	1,128	732	109.7	+25.1
	WV	837	423	897	613	102.4	+44.4
Pine	NY	3,912	332	564	426	31.1	–8.3
	PA	243	374	528	438	25.4	–6.6
	NJ	5,027	338	565	386	21.6	+29.2
	MD	2,640	326	508	420	29.1	+9.4
	DE	131	376	452	414	21.1	+6.1
	VA	16,447	316	752	441	29.8	–14.3
	WV	591	349	575	469	38.7	+14.8

	State	Grid no.	Wood NPP (g m^{-2} yr^{-1}, spatial N)				Δ% in mean (vs. FIA)
			Min	Max	Mean	STD	
HW	NY	59,062	424	923	691	76.2	+34.6
	PA	107,264	496	978	723	82.3	+32.5
	NJ	7,239	505	891	623	77.6	+24.9
	MD	8,182	488	801	578	36.5	–1.5
	DE	1,781	514	633	571	19.5	+7.0
	VA	46,410	456	1,145	654	107.1	+16.5
	WV	38,616	474	1,109	816	125.8	+49.0
SF	NY	208	355	441	398	17.2	+5.0
HW/Pine	NY	1,504	446	732	593	53.0	+29.4
	PA	7,988	436	757	567	72.2	+22.6
	MD	1,442	423	635	508	25.9	+6.1
	VA	17,806	386	919	532	57.4	–9.1
	WV	837	418	832	576	98.9	+35.6

Table 3. (continued)

	State	Grid no.	Wood NPP ($g\ m^{-2}\ yr^{-1}$, spatial N) Min	Max	Mean	STD	Δ% in mean (vs. FIA)
Pine	NY	3,912	328	559	427	31.6	–8.1
	PA	243	369	536	439	26.8	–6.3
	NJ	5,027	336	570	387	21.7	+29.6
	MD	2,640	325	507	420	29.0	+9.5
	DE	131	370	465	416	21.9	+6.5
	VA	16,447	318	749	441	29.8	–14.3
	WV	591	358	575	474	40.0	+15.9

in the high elevation that runs from northeast to southwest of the Mid-Atlantic region. This landform feature characterizes the pattern of foliar N concentration for deciduous forests (Figure 1A), high in the mountainous areas and low in the southeast lowlands. Thus, the predicted NPP is affected by the pattern of foliar N concentration and is low in the southeast area. This result opposes the concept that NPP is high in the southern region where temperature is higher and light is sufficient for growth. The latitudinal range for our study region covers 7°, and the difference of July mean temperature from the southern boundary to the northern boundary is only approximately 4.3° C. The elevations range from 450 to1200 m, and the air temperature can differ at the same latitudes 1.3–6.3° C from the lowlands. Foliar N concentration is related negatively to irradiance and is lower with longer-lived foliage associated with longer photoperiod (Field 1983, Chen et al. 1993, Yin 1993). Deciduous trees in high elevations experience lower summer temperature but receive slightly higher irradiance than the lowlands. Therefore, the spatial foliar N concentration equation that depends solely on July temperature may overestimate foliar N concentration in mountainous areas, which causes PnET-II to overestimate NPP in higher elevations.

Validation for the Model Predictions of Wood Production

We compared wood production between the PnET-II predictions and the estimates derived from FIA measurements at the state level (Table 3, Figure 3), with exclusions of some forest types that have few FIA sites within a state. The model overestimates wood production of deciduous forests by 47–75% when using the constant foliage N concentration parameters. The model either overestimated or underestimated wood production by –14–29% by state for coniferous forests (Table 3). The overestimated NPP for mixed forests, ranging from 21 to 44%, is likely caused by the overestimates for deciduous forests because PnET-II calculates the mixed forests as mosaics of deciduous and coniferous forests.

Using the equation-generated foliar N concentration data in PnET-II, we predicted a –2–49% difference in wood production for deciduous forests, a –14–30% difference for coniferous forests, and a –9–35% difference for mixed forests relative to the FIA estimates (Table 3). The comparison shows that the NPP prediction is improved by reducing 26% of the maximum difference from the FIA estimates when using spatially defined foliar N concentration data. The reduced difference ranges from 12 to 59% in different states. The improvement is obvious for several states in the southeast. However, the difference between the model prediction and the FIA estimate can be still as high as 49% in West Virginia, which is characterized by high elevations (Table 3). For the coniferous forests, the model predictions do not have obvious differences with alternative foliar N concentration data as inputs.

Except for New Jersey, PnET-II made reasonable predictions of wood NPP (–14–15% difference) for coniferous forest at state level (Table 3). This range is within an acceptable level for NPP predictions. A conservative estimate of errors associated with field measurements of NPP is approximately 20% (Pan et al. 1996). Thus, we considered the acceptable biases for model prediction of NPP to be 20% at the pixel scale (i.e., 0.5°), 10% at the biome scale, and 5% at the continental scale (Schimel et al. 1997, Pan et al. 1996). The acceptable biases for this comparison are likely within 10–20% because the NPP predictions were compared at state level, which aggregated information from pixels with much finer resolution (30″). Overestimates of wood NPP in New Jersey pine forests (30%) may be attributed to barren sandy soils in the state where field growth is poorer than the modeled conditions.

The comparison shows that using spatially defined foliar N concentration data with deciduous forests improved the model prediction of wood production in the southeast lowlands but still overestimated wood production in mountain regions (Figure 3). The foliage N concentration at high elevation is higher because of relatively lower summer temperatures in July. Higher foliar N concentration in colder areas was related to short-lived foliage and low foliage mass with the amount of passively concentrated N in foliage (Yin 1993). However, lifespans of deciduous foliage are determined primarily by both photoperiod and temperature (O'Neil and DeAngelis 1981). The temperature equation of foliar N concentration can cause an overestimate of foliar N concentration in high elevations where temperature and irradiance do not concurrently decline as in high latitudes. In addition, relatively severe acid deposition reportedly occurs at high elevations in the Mid-Atlantic region. Acid deposition could deplete soil nutrient cations and decrease

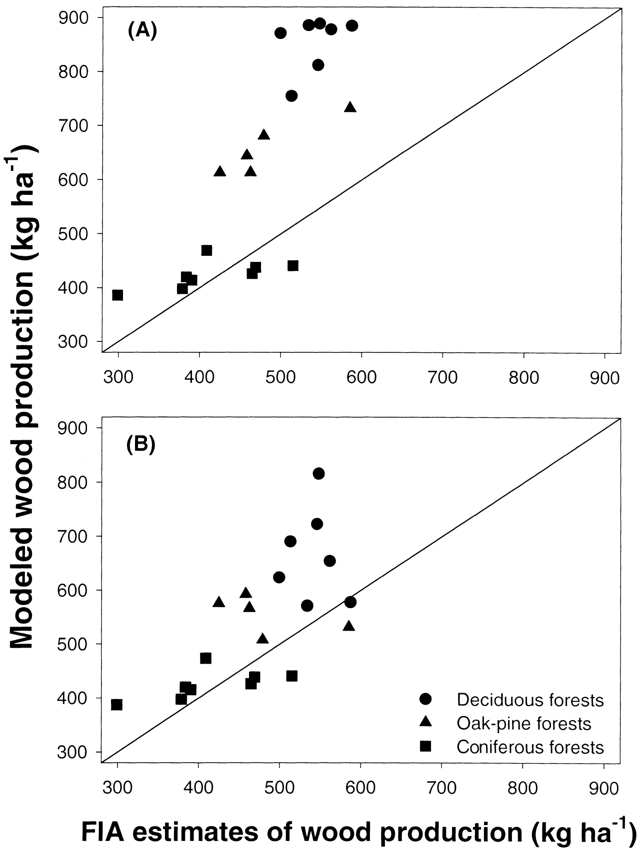

Figure 3. Comparison of wood production between the model predictions and the estimates derived from the FIA data for different forest types at state level. (A) The model predictions with constant foliar N concentration parameters; (B) the model predictions with the equation-generated spatial foliar N concentration data.

canopy N in those hardwood forests at higher elevations and affect tree growth (Hallett and Hornbeck 1997, Fenn et al. 1998).

Because PnET-II predicts forest productivity of mature forests without considering land-use history and disturbances, the improved but generally overestimated wood production for deciduous forests may be attributed to these factors, also. Meanwhile, FIA data represent broad ranges of forest conditions and probably actual values of growth (Birdsey 1992). Although the FIA data were selected from less disturbed sites in the last 10–14 years, the historic disturbances could still affect N cycling and cause decreased foliar N concentration in trees (Ollinger et al. 2002). The FIA estimates appear to have a wider range of variations than the model predictions (Table 3), which may reflect diverse effects of land-use history and local environmental conditions. The effects seem to influence deciduous forests only. The model shows that PnET-II predicted wood NPP well for coniferous forests, regardless of foliar N concentration. Deciduous forests respond more to increased N than coniferous forests that have less capacity (Reich and Schoettle 1988, Waring and Schlesinger 1985, Yin 1993, Ollinger et al. 2002).

Conclusion

This study uses alternative foliage N data to parameterize the PnET-II model, revealing that wood production of deciduous forests is sensitive to canopy foliar N concentration. Spatial foliar N concentration, generated by the foliar N concentration equations (Yin 1993), varies widely for deciduous forests across the region and only slightly for coniferous forests. When using constant foliar N concentration parameters as the input, the model overestimates wood production for deciduous forests by 47–75% at the state level but predicted reasonably for coniferous forests. Replacing the model inputs with the spatial foliar N concentration data improved the prediction of wood NPP significantly for deciduous forests but barely affected the prediction for coniferous forests. Based on the FIA validation, the improvement for predicting deciduous wood NPP increased 17% at the regional scale and 12–59% at the state level. The improvement in the model prediction was greater for those states in the southeast lowlands than those with high elevations.

Although the prediction of wood NPP for deciduous forests improved greatly, the model still overestimates wood NPP for some states with unacceptable biases (24-49%). The temperature-related foliar N concentration equation for deciduous forests may overestimate foliar N concentration in high elevations where irradiance is much higher than the corresponding latitudes with similar temperature. The overprediction in N is likely responsible for overestimating wood production by the model such as in West Virginia (49%). Several other factors may also contribute to the model's overestimate of wood production for deciduous forests (e.g., N-leached sandy soils in New Jersey, acid deposition, and historically intensive land uses in the region). These factors are likely to affect N cycling and foliar N concentration but are not incorporated in current model predictions.

Validation in this study is useful to reveal both rationality and problems in the model predictions and provide possible solutions for a better model prediction. The validation suggests that spatially explicit and accurate data of foliar N concentration are critical to modeling deciduous wood production by PnET-II in the Mid-Atlantic region. The foliar N concentration equation applied in this study may be appropriate for generating data across a wide geographical range. However, for the region scale, such as the Mid-Atlantic where temperature pattern is more controlled by elevations than latitudes, a more regional foliar N concentration equation needs to be developed to reflect a special pattern of foliar N concentration distribution that is associated with temperature and photoperiod. Collecting data of foliar N concentration along relevant climate gradients in the region will help to develop better regional foliar N concentration equations and advance the model prediction of forest productivity. Uncertainty in the prediction may decline if the model incorporates spatial effects of acid deposition and land-use history, also.

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