

# Synthesis and Extrapolation

## *Models, Remote Sensing, and Regional Analysis*

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and S. OLLINGER

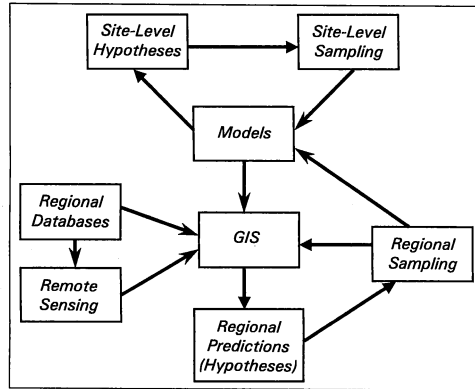
### **Introduction and Background**

How relevant is the research we do at the Harvard Forest to the larger New England region we claim to represent? Most of our experiments are set in forests we consider “typical,” but all show sensitivity to site conditions, species, or history—all three of which vary widely across the region. How can we extrapolate across time and space to make useful predictions into the future? “Regionalization” of results from individual sites or studies has been a core concern of the LTER program for many years. How do we contribute to this goal?

At the first All-Scientists’ Meeting of the LTER program in 1991, we proposed an approach that would tie intensive, site-level research to predictions across New England and into the future (modified in Figure 17.1). This approach embodies the traditional steps in scientific research: data acquisition, synthesis of information into a set of working theories, and generation of hypotheses to be tested out of those theories. The figure, though, includes two loops: one for intensive site work and another for extensive or regional work. These two are linked through a box called “Models.”

By “models” we mean computer models that represent ecosystem processes as a series of linked equations. In our approach, those equations come directly from statistical analyses applied to collected data. Models are formed by tying together the results of different field research projects expressed usually as regression equations between some environmental factor (for instance, light) and an ecosystems process (for instance, photosynthesis).

Several different models, operating over very different scales of time and space, have been developed as part of the Harvard Forest LTER program, but all of them share a common approach. Harvard Forest models tend to be strongly empirical, combining measured data with the cur-



**Figure 17.1.** A conceptual approach to the integration of intensive site-level research and extensive regional-scale research with spatial data sets within a geographic information system (GIS). Note that models of ecosystem function are the integrating focus of this approach. Based on Aber, Driscoll et al. 1993.

rent understanding of the physiological processes involved. They are generally data-rich and well-tested, or validated, against additional measurements not used to derive the model. Our more complex models are not calibrated, in that the input parameters are not “tuned” in order to achieve better agreement between model predictions and measurements. Rather, discrepancies between predictions and observations are taken for what they are—indications of incomplete or erroneous understanding of the processes involved (Box 17.1).

To regionalize Harvard Forest results, then, we run these models derived from field research (the upper loop in Figure 17.1) using information on the regional variation in factors such as temperature, radiation, or precipitation that drive the processes. Both input data and model outputs are managed through a geographic information system (GIS), essentially a digital map of the region (several sample outputs are shown below). Maps of model predictions are essentially hypotheses stated at the regional scale. We also test these where the data exist, as we have for forest production and stream flow. Disagreements between predictions and measurements at this level also provide insights into how the models can be improved (Figure 17.1) or how good they might actually be at predicting our collective future.

### **From Simple to Complex Models of Ecosystem Processes**

This process of model development and refinement can best be illustrated through several examples from the Harvard Forest. These

### **Box 17.1.**

While the use of models is widespread in broadscale ecological predictions, such as biotic responses to global change, many ecologists remain skeptical of the modeling process and tend to disbelieve or discount insights provided by modeling exercises. In this way, ecology differs from many other scientific fields in which quantitative model predictions, and verification of those predictions, are central.

There may be a good reason for this general distrust of models in ecology: modeling projects and modeling papers are not universally held to a consistent, rigorous set of standards of full disclosure during peer review, especially as compared with data papers. We have proposed two achievable objectives that could help increase the value of the modeling process in ecological research: (1) establish a set of guidelines or standards by which papers presenting modeling results should be judged, and (2) increase clarity in the understanding of the difference between calibration and validation.

On the first point, all modeling papers should contain, at a minimum, the following sections, with the suggested content:

- **Model Structure:** The diagram or schematic should be complete with all components and connections shown. More important, the equation(s) used for each connection should be stated explicitly or clearly referenced, and citations should be given justifying that equation form. If the equation is theoretical or invented, this should be stated and justified on the grounds that no data were available on this process. This section of the paper should become a literature review of previous work on the processes modeled, thus ensuring that the modeler is aware of previous field and laboratory work. The modeling process and literature review may suggest an equation form not previously used in presenting empirical results, which can be a major contribution of the modeling process.
- **Parameterization:** *All* of the parameters used in the model should be listed (with units), and all values for those parameters given, along with references to the sources of those parameters. If the parameters

are derived by calibration, this should be clearly stated, the calibration method described, and the calibrated values given. If the model is mostly a theoretical construct used for identifying questions, this should be stated explicitly. However, whenever possible, models should include realistic, empirically based parameterizations that tie the model as closely as possible to experimental data.

- **Validation:** *No modeling paper should be accepted without at least some attempt to compare model predictions against independent data sets, that is, data not used in any way in the derivation of the model's parameters. Ecology is data-rich and model-poor relative to other fields. There are very few aspects of ecology for which no validation data exist. Where this is the case, such as with predictions of large-scale phenomena for which experiments cannot be run, this should be explicitly stated by the authors. Even in such models there are often intermediate variables that are predicted by the model and for which independent experimental data can be found.*
- **Sensitivity Analysis:** *Every modeling paper should present the effects of altering model parameters or input variables on model predictions to give the reviewers some idea of model responsiveness to such changes. This also provides information on the importance of specifying each variable correctly. A greater degree of uncertainty can be tolerated in parameters to which the model is relatively insensitive. A second type of sensitivity analysis might be called the "null model" approach, stated as, "How does the predictive ability of the model compare with that of a simple multiple linear regression model?" Stated another way, what is the increase in predictive accuracy achieved by moving from a statistical model to one that includes knowledge of the processes in the system?*
- **Prediction:** *Only after the above standards have been addressed should the model be used to predict something. Perhaps the greatest disservice ecologists can provide comes from allowing poorly described and invalidated models to be used to predict the results of policy actions. This is equivalent to basing policy decisions on data we know to be seriously flawed. It also fosters the false impression that we know more than we do about the systems we study, which is then often in contradiction to what the experimental data suggest.*

### **Box 17.1. continued**

On the second point, all model papers, and all reviewers of models, should be clear on the distinction between "calibration" and "validation." They are two distinct sides of the modeling coin, as opposed as night and day, and cannot be substituted one for the other. Calibration is the use of information on system behavior or outputs to derive parameters within the model. If all measurements are used in the calibration process, then no independent data sets are left for validation, the comparison of model predictions against independent data sets not used in deriving the parameters. Calibration is thus a method for deriving parameters for the model, while validation is a comparison of model predictions with additional, independent data sets.

Unfortunately, the calibration process can be abused in ways that remove the chance for one to gain insights into ecological processes through modeling. In the worst applications of the calibration process, a model with  $n$  parameters is calibrated to  $n/10$  or  $n/20$  measured output variables by manipulating parameter values until the model predictions match those few measured values. While parameter manipulation might be done in a subjective way through adjustments by the model user, or in an objective way by various Monte Carlo or other randomized search methods, the result still contains what in statistics would be called a serious problem of negative degrees of freedom. Often, many, many sets of derived parameters would give the same result. There is a very strong realization of this among those who do not do modeling, and the charge is always raised that modelers can produce any outcome they desire. Using the calibration procedures described here, that is the case. When the parameters derived by this procedure are not fully reported, this sense of lack of rigor is reinforced.

Perhaps one of the worst characteristics of a calibrated model is that it cannot fail. With negative degrees of freedom, accurate prediction of the few output variables is assured. When models cannot fail, we cannot learn from them. We cannot, then, use models to frame questions and to help derive future research programs. The modeling process becomes sterile and unenlightening.

We can at least provide this degree of rigor to calibrated models: require that the model predictions be compared against totally indepen-

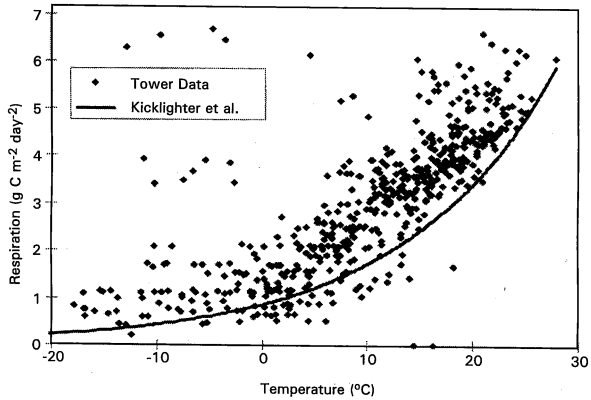
dent data. The validation step can be applied to a calibrated model, as the two steps, calibration and validation, are distinct. One is a method for deriving parameter values and the other is a method for assessing the accuracy of the model, at least within the bounds of the validation data set.

In a pure case of a validated model, the parameters are derived directly from published data and the model is then run, without parameter modification, and predictions are compared with additional published data to see how well model predictions match those data. If the agreement between predicted and observed is not "good," that is an interesting and useful result, suggesting that our knowledge is imperfect. Analyses of why the model "failed" can suggest where future research should be focused to reduce uncertainties in our understanding of the integrated response of an ecological system. In addition, by knowing that a model can fail, we can then have more confidence in it when it does succeed. (Adapted from Aber 1997, *Bulletin of the Ecological Society of America*)

will be presented in order of increasing complexity—from single-factor regression equations to integrated models that contain interactions (feedbacks) among several different processes.

### *Soil CO<sub>2</sub> Flux*

Intensive measurements of daily soil CO<sub>2</sub> efflux made using static chamber techniques as part of the soil-warming experiment (Chapter 13) form a core data set in a global analysis of the effect of soil or air temperature on soil respiration (Figure 17.2). Carbon dioxide flux data from the EMS tower (Chapter 10; Figure 17.3) provided a unique opportunity to test this relationship against data collected by a totally different technique covering a very different spatial scale. Results compare favorably (Figure 17.2). The chamber data are consistently lower than the tower data because they do not include respiration by aboveground plant tissues. This relationship is used in more complex models applied to the Harvard Forest.



**Figure 17.2.** Relationship between soil temperature and soil CO<sub>2</sub> efflux for temperate deciduous forests: comparison of total ecosystem respiration measurements at the eddy covariance tower on Prospect Hill (data points) with values predicted by summary equations using data from several sites around the world (line; Kicklighter et al. 1994). The effects of temperature are similar in both relationships, whereas total respiration is higher from the eddy covariance data because of inclusion of aboveground (tree) respiration. Modified from Aber et al. 1996, 261: fig. 4, with permission from Springer-Verlag (copyright 1996).

### *Methane Consumption in Forest Soils*

Measurements of methane consumption in soils at the Harvard Forest have been made in the chronic nitrogen plots under ambient conditions throughout the frost-free season over a six-year period. In addition, experimental water-exclusion and water-addition experiments have been carried out in subplots within and adjacent to the manipulated areas. Together, these data sets cover a range of conditions of soil moisture, temperature, and nitrogen availability and allow a multifactorial analysis of controls on this important process.

Field data show that methane consumption (1) increases with increasing temperature, (2) decreases as water-filled pore space (WFPS or soil water content) increases from 20 percent to 100 percent (Figure 17.4), and (3) is very sensitive to nitrogen availability in soils, having declined by 25 percent in the first year of the chronic nitrogen experiment, moving to a 64 percent reduction by Year 6 (Chapter 12).

A multiple factor model built to predict methane consumption based on these relationships has been applied globally at the  $0.5^\circ \times 0.5^\circ$  scale. Using this model, we estimated that soils consume about 100 teragrams per year at the global scale. This estimate is about twice the previous estimates of the strength of the global soil methane sink.



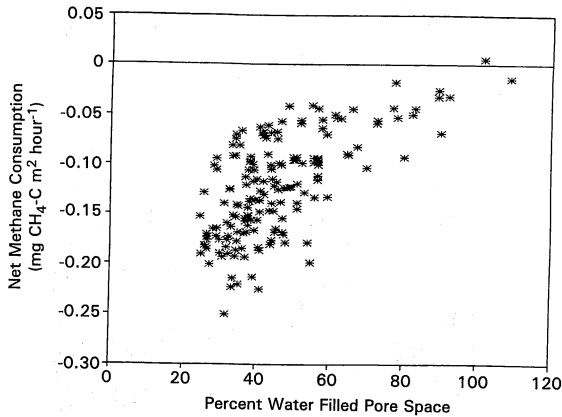
**Figure 17.3.** An eddy flux system that records exchanges of  $\text{CO}_2$  and other material between the forest and the atmosphere. One of three such systems in operation at the Harvard Forest, this equipment is situated above an old-growth hemlock forest in the center of the Prospect Hill tract. Results are compared with detailed physiological and ecosystem results and are being used to develop a simple model of forest ecosystem function. The canopy walk-up tower used for this system also provides access to leaves, branches, and boles of the tree for detailed physiological measurements. Photograph by J. Gipe.

### *Whole-Canopy Gross Photosynthesis*

The long-term, continuous eddy covariance gross and net carbon exchange data available for the Harvard Forest offer a unique opportunity to challenge whole-canopy models of forest photosynthesis. The daily summations of gross photosynthesis, or gross ecosystem exchange (GCE, Chapter 10), are accompanied by direct measurements of temperature, radiation, and other climatic parameters that affect these processes.

The PnET-Day model predicts daily gross and net photosynthesis using an empirical relationship between foliar nitrogen concentration and maximum potential photosynthesis ( $A_{\text{max}}$ ), a similar relationship between photosynthesis and stomatal conductance (see Chapter 3), along





**Figure 17.4.** Effects of soil moisture (expressed as percent water-filled pore space) on net methane consumption at the Harvard Forest. As soil moisture increases, methane consumption in the soil declines and more methane is released to the atmosphere, where it can serve as an important greenhouse gas. Modified from Castro, Steudler et al. 1995, 6, with permission of the American Geophysical Union (copyright 1995, American Geophysical Union).

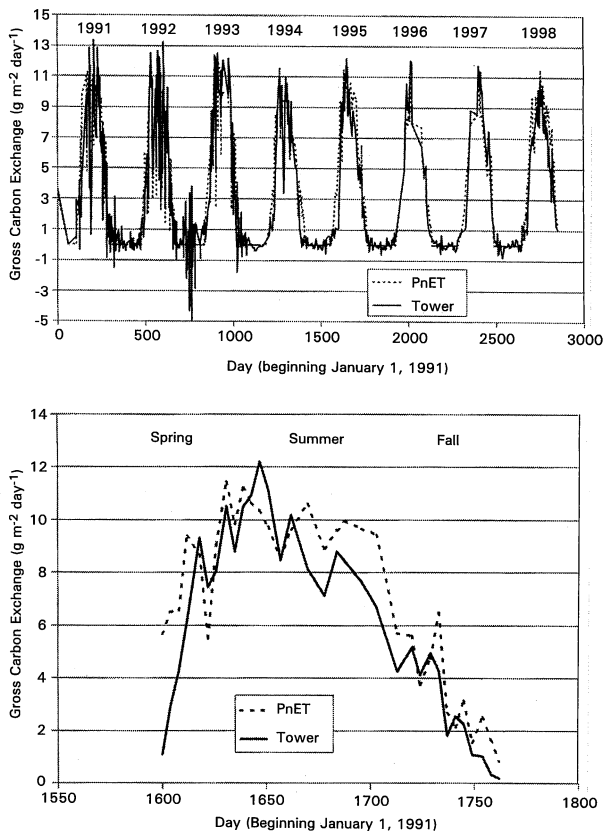
with standard functions for response to radiation intensity, temperature, and vapor pressure deficit in conjunction with daily climate data to estimate gross and net photosynthesis and potential evapotranspiration.

Comparing PnET-Day predictions of daily gross photosynthesis with values measured at the EMS tower is a good example of model testing or validation (Figure 17.5, top). The mean difference between predicted and observed is 0.13 grams carbon per square meter per day or 3.7 percent of the daily mean GCE of 3.45 grams carbon per square meter per day.

Models are also interesting when they fail. PnET-Day does not calculate water stress. During a significant period of drought in August of 1995, PnET-Day predictions were higher than observed GCE values by 1 to 2 grams carbon per square meter per day (Figure 17.5, bottom), suggesting that water stress was indeed important during this period and that the model needs to include this factor.

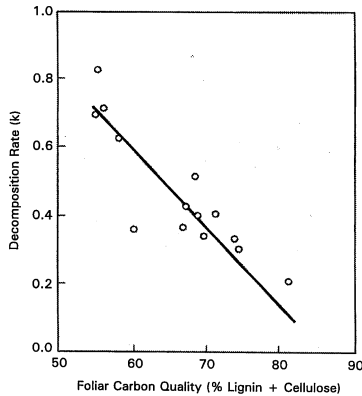
#### *Litter Decomposition and DOC/DON Flux*

The first field studies of litter decomposition at the Harvard Forest were carried out nearly twenty-five years ago. Overall, several thousand small bags constructed from fine-mesh materials and containing senescent plant tissues of various kinds have been placed out in the forest, retrieved after different periods of time, and analyzed for chemical



**Figure 17.5.** Comparison of gross carbon exchange estimates by the PnET-Day model with measurements at the eddy covariance tower for the period 1991–1998 (top) and expanded view of data from the summer of 1995 (bottom). Based on Aber et al. 1996.

content. Predictive equations describing both the rate of mass loss and the gain or loss of nitrogen during decomposition have been developed, using carbon quality or the chemical composition of the material as the driving variable (Figure 17.6). In general, decomposition rate decreases with increasing content of lignin (a complex phenolic compound that encrusts cell walls, making wood woody and oak leaves leathery) and increases with increasing content of materials that dissolve in hot water (“extractives,” including sugars, starches, and amino acids). Cellulose, the primary constituent of cell walls and probably the most common biopolymer in nature, decays at intermediate rates unless “protected” by lignin. We now know (see Chapter 12) that not all mass loss from litter occurs through conversion to CO<sub>2</sub> by microbial decay. A significant fraction of carbon loss can occur in dissolved form as dissolved organic



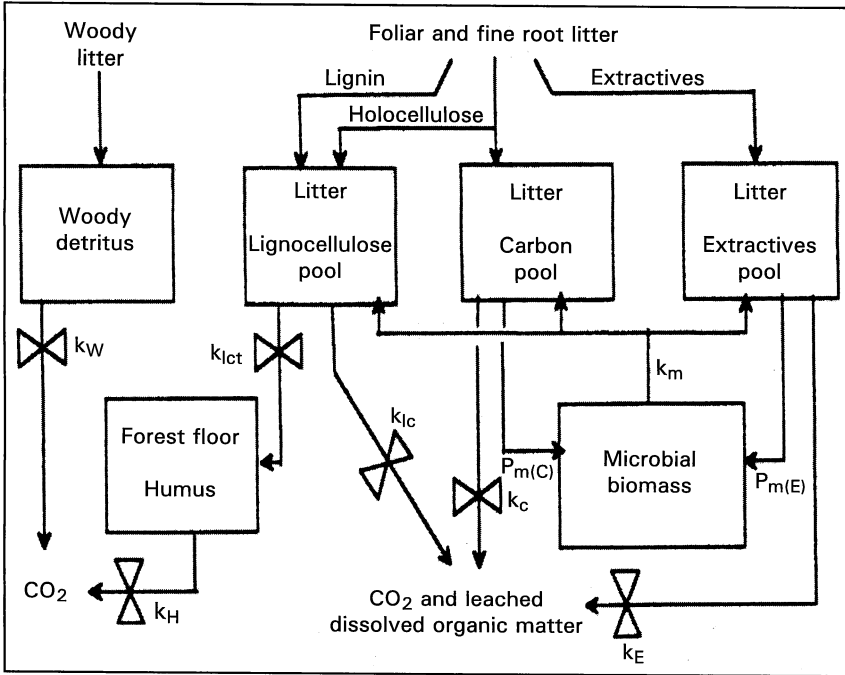
**Figure 17.6.** Summary relationship between the carbon quality of different types of foliage and their decomposition rates. The “k” value is an expression of the speed of decay. Lignin plus cellulose is the sum of these two carbon fractions (equivalent to 1 – extractives, or the soluble carbon content) in litter. Modified from Aber et al. 1990, with permission from NRC Research Press.

carbon, or DOC. Similarly, fluxes of DOC from the forest floor to the mineral soil and on to streams and groundwater have received increasing attention.

DocMod (Figure 17.7) is a model that predicts litter decay rates based on the carbon quality and nitrogen content of different materials, dividing plant materials into their extractive, cellulose, and lignin-cellulose components. These three materials decay at different rates, producing various amounts of CO<sub>2</sub>, DOC, dissolved organic nitrogen (DON), and stabilized organic matter (humus) in the process. Decay rates are modified by temperature and moisture using actual evapotranspiration (AET) as a surrogate. Nitrogen dynamics are driven by decay rates, microbial carbon-use efficiencies for each class, and resulting nitrogen release or immobilization.

The model was linked to a GIS and applied to the White Mountain region of New Hampshire using spatial models for climate and forest production generated by other regional models (see regional PnET discussion below). The linked DocMod-PnET model predicted spatially explicit patterns in forest floor mass and nitrogen content as well as CO<sub>2</sub> and DOC and DON fluxes. Across elevational ecotones in vegetation communities in the region, the linked DocMod-PnET model accurately predicted increases in DOC and decreases in CO<sub>2</sub> efflux with increasing conifer content in forests, due to temperature gradients and increases in low-quality carbon content (lignin) in litter. DocMod was also found to be robust in a modeling intercomparison of blind predictions of litter

## DocMod Model

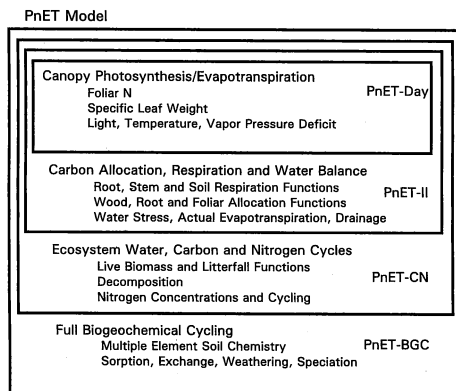


**Figure 17.7.** Structure of the DocMod model showing carbon fluxes. The variables  $k_W$ ,  $k_H$ ,  $k_{lc}$ ,  $k_E$ , and  $k_C$  represent decay rates for woody detritus, humus, lignocellulose, extractives, and unprotected cellulose, respectively. The variable  $k_m$  represents turnover of microbial biomass, and  $k_{lct}$  indicates lignocellulose transfer, the movement of mass from the lignocellulose pool to the humus pool.  $P_{m(C)}$  and  $P_{m(E)}$  indicate production of microbial biomass from substrates in the unprotected cellulose and extractives pools. Modified from Currie and Aber 1997, with permission from the Ecological Society of America.

decomposition across four terrestrial ecosystems in the LIDET study (LTER Intersite Decomposition Experiment Team).

## Ecosystem Models

Equations that summarize individual processes need to be linked together to capture the dynamics of whole ecosystems. For example, if photosynthesis in PnET-Day is linked to the concentration of nitrogen in foliage, then changes in the decomposition processes in a model like DocMod will change foliar nitrogen and total carbon gain for the forest. Conversely, changes in photosynthesis will alter the production of litter, which will alter decomposition rates.



**Figure 17.8.** The nested structure of the PnET models showing the various ecosystem functions that are added with each layer of complexity.

### *The PnET Models*

The PnET family of models are actually a nested set of algorithms of increasing complexity for predicting carbon, water, and nitrogen cycling in temperate and boreal forests (Figure 17.8). The simplest core model is PnET-Day (discussed above), which calculates gross and net photosynthesis. This is embedded within PnET-II, which adds a water balance routine, including water stress and carbon allocation and respiration algorithms. PnET-CN adds pools for woody biomass and soil organic matter and routines for litter production and decomposition, as well as adding nitrogen content to all pools and fluxes. The advantage of this approach is that the simpler versions require fewer input parameters to run. So, for example, if only daily photosynthesis values are of interest, only about one-third as much information is required to run the model, in comparison with the full PnET-CN version. PnET is an open-code project (code available at [www.pnet.sr.unh.edu](http://www.pnet.sr.unh.edu)). Each of the versions of PnET has been applied at the Harvard Forest and also at the Hubbard Brook LTER site in New Hampshire.

PnET-II has been tested against data on monthly carbon balance as measured at the EMS tower and against annual foliar and wood production in the control plots of the chronic nitrogen amendment experiment (using measured foliar nitrogen values for the area around the tower and in the plot itself, respectively). In the chronic nitrogen plots, PnET-II predictions for wood and foliar production on these plots are within 10 percent of measured values (Table 17.1; again, input parameters have not been calibrated in any way). The relatively low productivity values for the hardwood control stand reflect the relatively low measured foliar nitrogen concentration (2.0 percent).

**Table 17.1.** Predicted (PnET-II) and Observed Values for Wood (Aboveground Plus Woody Roots) and Foliar Production at the Control Plots in the Chronic Nitrogen Stands

	Pine			Hardwood		
	Foliage	Wood	Total	Foliage	Wood	Total
PnET-II (no O <sub>3</sub> )	307	341	648	294	527	821
PnET-II (with O <sub>3</sub> )	280	301	581	284	430	714
Measured	316	310	626	300	475	775

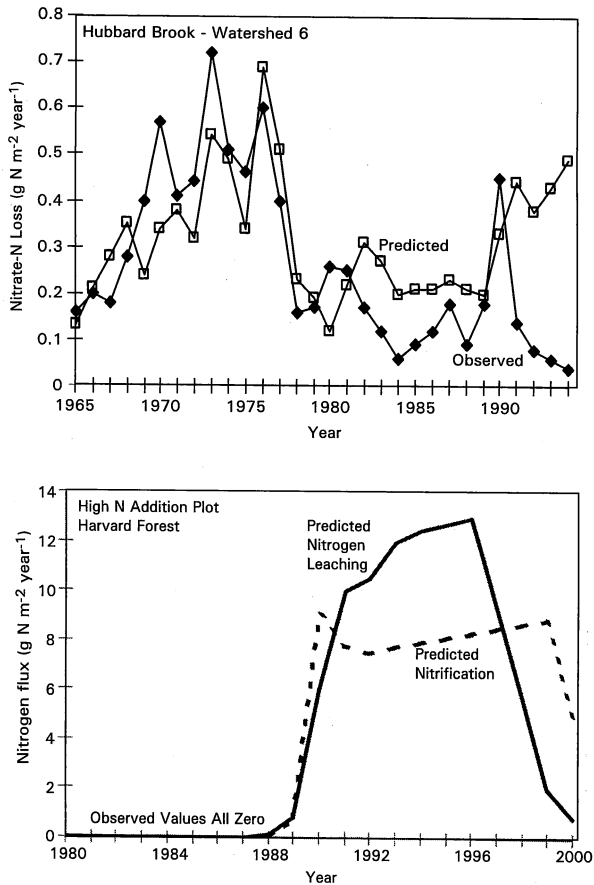
*Note:* Units are grams of biomass per meter square per year. Both measured and predicted productivity data are for the period from 1988 to 1996. Estimates for net primary production with ozone effects use the algorithms presented in the regional applications section in the text.

As discussed below, ground-level ozone is a potentially important stressor for forests in central New England. Our PnET estimated net primary production (NPP) values have always been slightly above the measured values. Using the algorithms for ozone effects on photosynthesis described in the regional modeling section below as well as measured ozone concentrations at Ware, Massachusetts, we tested the predicted effect of ozone on NPP (Table 17.1). These predictions are now slightly below measured values. The area around Ware has among the highest ozone concentrations in New England, and values from this site may be too high for the nearby Harvard Forest site, which is at a higher elevation and is heavily forested.

PnET-CN incorporates the long-term effects of land-use and disturbance history on ecosystem function by adding long-term storage pools (wood and soil organic matter). As a result, this version requires an accurate description of site history and offers insights into the duration and nature of disturbance effects.

Two different tests of the PnET-CN model have yielded very different results. At Hubbard Brook, the model successfully captures the major features of the long stream nitrate record in the reference watershed (W6) once both variation in climate and all the biotic and abiotic disturbances known for the watershed are included (Figure 17.9, top). This is a fairly rigorous test as nitrate loss to streams is a small net flux that is the difference between many large gross fluxes (for example, mineralization and plant uptake).

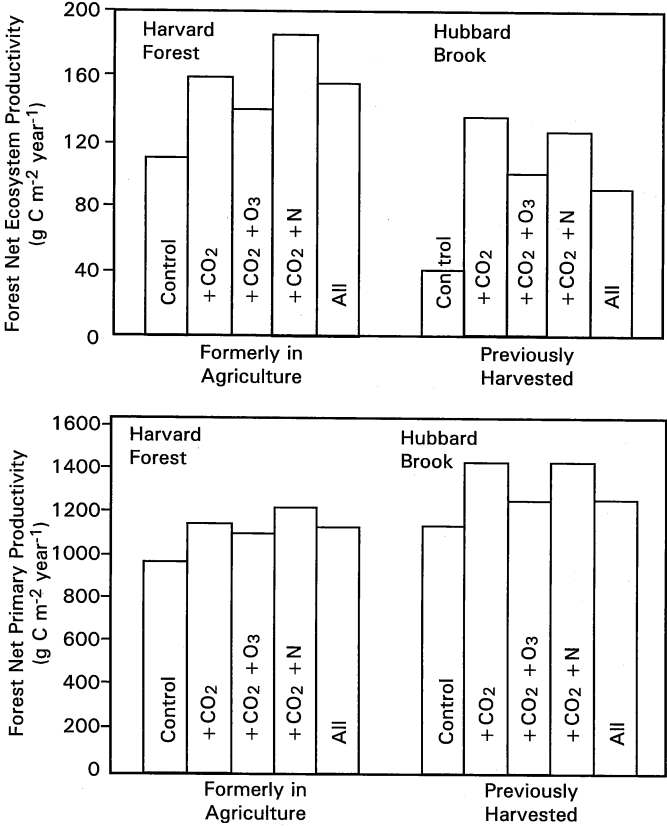
In contrast, the model fails miserably when tested against the nitrate loss record for the high-nitrogen treatment in the hardwood stand of the chronic nitrogen experiment (Chapter 12). That forest captured and retained nearly all of the 100+ grams of nitrogen added per square meter over the first eight years. PnET-CN with monthly fertilizations during the growing season equivalent to those applied in the chronic nitrogen experiment predicted immediate and very large losses of nitrate (Figure 17.9, bottom).



**Figure 17.9.** Predicted and observed annual nitrate flux below the rooting zone and into streams or groundwater as predicted by PnET-CN. Two examples are shown: the reference watershed (W6) at Hubbard Brook (top), and the high nitrogen addition plots in the hardwood stand at the Harvard Forest chronic nitrogen addition experiment (bottom). Measured values are all zero. Top panel modified from Aber et al. 1997, 69, with permission from Elsevier Science (copyright 1997); bottom panel based on Aber and Driscoll 1997.

We learn as much or more when models fail as when they succeed. This lack of agreement shows that there is a process of nitrogen retention operating in the chronic nitrogen plots that we do not understand and have not included in our models (see Chapter 12 for a discussion of several possibilities). Understanding and measuring these processes so that they can be described quantitatively and added to PnET would increase the completeness of the model and the accuracy of predictions at high rates of nitrogen application.

Using models as consistency checks on our understanding of ecosystems processes is a valuable application, but federal agencies generally fund models for their predictive capacities. Along with nitrogen deposition, increasing concentrations of ozone and CO<sub>2</sub> in the atmosphere are important components of the changing environment at the Harvard Forest. By adding relationships to PnET that capture current physiological understanding of the effects of these two gases on photosynthesis, and running the model for different land-use histories at the Harvard Forest (intensive agriculture) and Hubbard Brook (harvest only), we can predict the interactive effects of disturbance history and atmospheric chemistry (CO<sub>2</sub>, ozone, and nitrogen deposition). These effects are compensatory rather than reinforcing (Figure 17.10). Both nitrogen deposi-



**Figure 17.10.** Predictions from the PnET model for the effects of various combinations of CO<sub>2</sub>, ozone (O<sub>3</sub>), and nitrogen deposition as conditioned by land-use history at the Harvard Forest (extensive agricultural use) and at Hubbard Brook (forest harvesting only) on total carbon balance (net ecosystem productivity) and total plant production (net primary productivity). Modified from Ollinger et al. 2002, with permission from Blackwell Science Ltd. (copyright 2002).



tion and increased  $\text{CO}_2$  lead to increased forest production (NPP) and greater carbon storage (net ecosystem production, NEP), but these effects are more pronounced after nineteenth-century extractive agriculture at the Harvard Forest than in the harvest-only history at Hubbard Brook. In both cases, increased ozone offsets some of these gains.

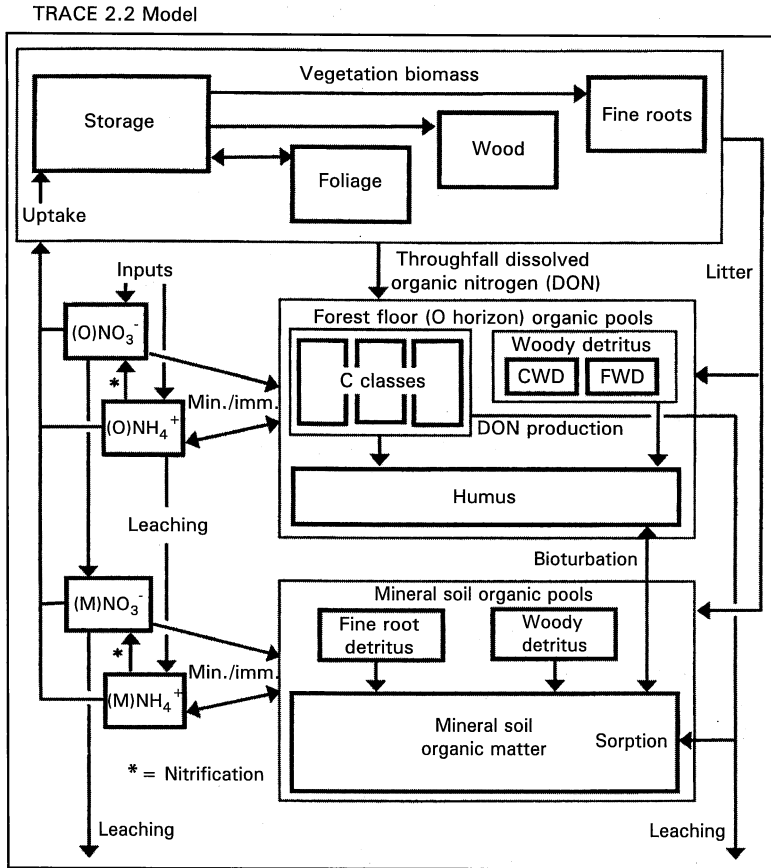
### *The TRACE Model of $^{15}\text{N}$ Dynamics*

PnET-CN could not predict or explain the continuing high rate of nitrogen retention in the chronic nitrogen plots. It also does not incorporate the information available from the  $^{15}\text{N}$  tracer studies applied in these plots or make use of the more complete description of the decay process included in the DocMod model.

The TRACE model (Tracer Redistributions Among Compartments in Ecosystems) was developed as a tool for interpreting processes controlling ecosystem-level redistributions of  $^{15}\text{N}$  at the Harvard Forest. It links plant processes of the PnET-CN model with soil submodels derived from the DocMod model described above (Figure 17.11). Plant and soil pools of carbon and nitrogen in TRACE are physically meaningful, in most cases designed to allow straightforward comparison with field or laboratory sampling methods. In one major structural change from PnET-CN, there are separate compartments for the forest floor and mineral soil horizons.

TRACE was first used to interpret mechanisms underlying plant-soil partitioning of  $^{15}\text{N}$  over a two-year period following the additions of  $^{15}\text{NH}_4^+$  and  $^{15}\text{NO}_3^-$  tracers in the chronic nitrogen plots. In an iterative sequence of comparisons between model predictions and field data, alternative formulations of soil sinks for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were tested to account for measured distributions of  $^{15}\text{N}$  in soils and vegetation as observed in the field. Reasonable agreement between model predictions and field data required high gross rates of  $^{15}\text{N}$  assimilation from inorganic nitrogen pools by detritus (and associated microorganisms) for both  $^{15}\text{NH}_4^+$  and  $^{15}\text{NO}_3^-$  additions to ambient (nonfertilized) and chronically fertilized plots. The modeled plant uptake of  $^{15}\text{N}$  (verified by plant tissue concentrations of  $^{15}\text{N}$ ), followed by litter production, could not account for the high rates of  $^{15}\text{N}$  incorporation into organic fractions in soils. This finding was significant as it indicated strong soil sinks for  $\text{NO}_3^-$  in deciduous and coniferous stands at the Harvard Forest, in agreement with some, but not all, findings elsewhere.

Perhaps of equal importance was something TRACE taught us when it failed. To capture the very high rates of immobilization into litter required to match measured  $^{15}\text{N}$  redistributions, nitrogen assimilation into combined detrital-microbial pools had to be decoupled from the traditional concept of carbon bioavailability in litter pools. In other words, the very high rates of nitrogen immobilization and retention ob-



**Figure 17.11.** Schematic diagram of the hierarchical structure of pools and fluxes of nitrogen in the model TRACE 2.2. Plant uptake of nitrogen, detrital nitrogen dynamics, and nitrogen transformations are calculated separately in each soil layer. Pools of available nitrogen are separated by soil layer. O, organic horizon; M, mineral soil; CWD, FWD, coarse and fine woody detritus; Min./imm., mineralization and assimilation. Inputs =  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in atmospheric deposition, fertilizer, and isotopic tracer additions. For clarity, not all fluxes are shown in detail. Modified from Currie and Nadelhoffer 1999, 7: fig. 1, with permission from Springer-Verlag (copyright 1999).

served in the chronic nitrogen plots cannot be modeled using traditional views of carbon-use efficiency and biomass production by free-living microbes. This indirectly supports the hypotheses in Chapter 12 that this immobilization occurs through either abiotic or nontraditional (for instance, mycorrhizal) microbial processes. This direct and not fully understood process for nitrogen immobilization was the most important pathway for nitrogen immobilization into soil organic matter.

## Modeling the Effects of Environmental Change at the Regional Level

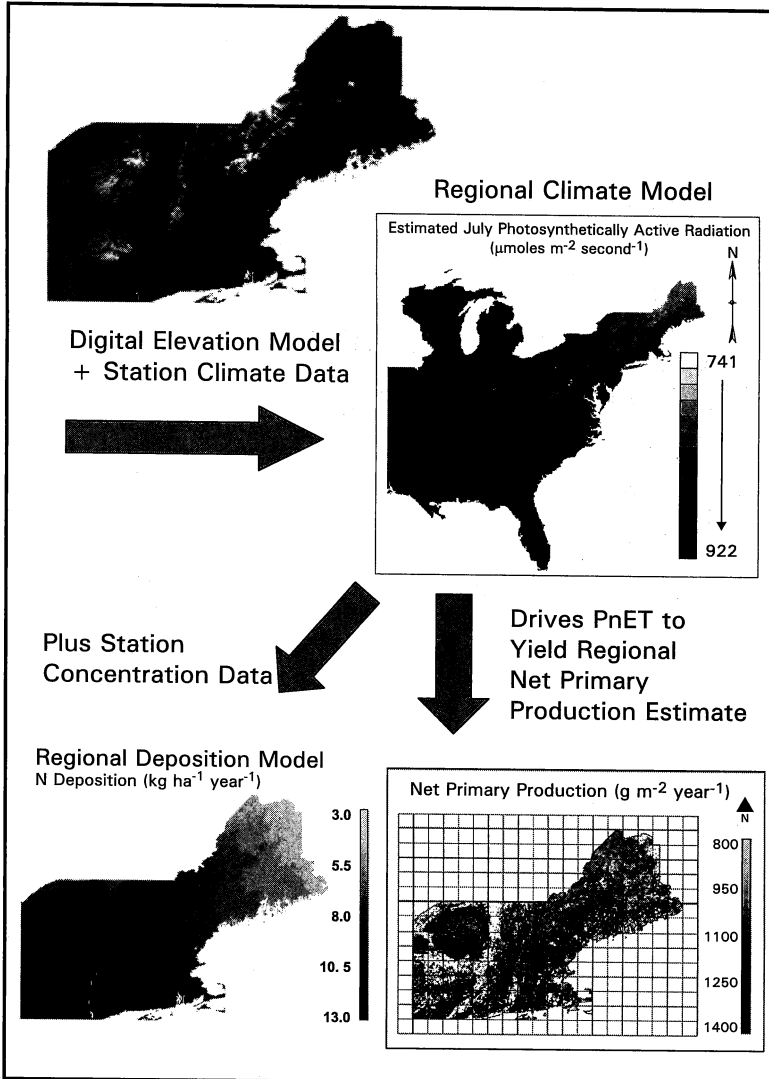
If models give reasonable results for intensively studied sites, how can we then extrapolate those results across whole regions? The concept is simple: specify all of the input parameters required by the model and it can be run anywhere. The reality, however, is more difficult and relates to model structure. The more complex the model, and the more input parameters required, the more difficult it will be to run at poorly studied sites or across broad regions. Said another way, the model can be run only for those locations where all the input parameters can be specified (or estimated).

We recognized this potential limitation when constructing the logic behind Figure 17.1 and designed the PnET models to be as simple as possible and to require as few inputs as possible. The goal was to capture most of the dynamic of forests in the region with the fewest possible parameters. Still, we need spatial information on climate and vegetation type across the region, and the accuracy of these spatial data sets are as important as the realism of the physiological functions within the model.

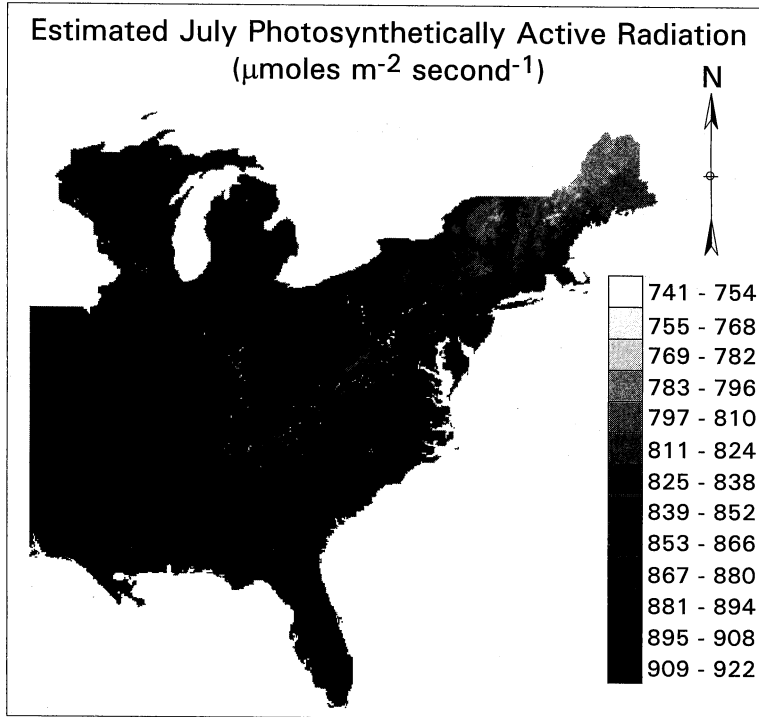
We have based our system for predicting climate in the New England region (Figure 17.12) on a digital elevation model (DEM), or an electronic map of regional topography. Simple regression models using data from more than 300 weather stations across the region predict mean temperature and precipitation as a function of latitude, longitude, and elevation yield estimates with mean errors of less than 1.5°C and 0.67 to 1.25 centimeters per month. These equations are then mapped back on to the DEM to yield spatial images of climate variables for the region (Figure 17.12).

It is interesting that the high-density data sets available for temperature and precipitation are not replicated for solar radiation. Even primary weather stations record only a crude “percent sunlight” value that approximates the fraction of any day with sunlight intensity above a certain value. Extensive solar energy monitoring networks initiated in the 1950s were discontinued in the 1970s. However, these older data sets can also be related to geographic location and used to derive seasonal and regional changes in solar energy input (Figure 17.13).

Mean monthly deposition of elements and ions in precipitation, averaged over several years, can be predicted from regional concentrations multiplied by predicted precipitation rates. For example, the concentrations of both nitrate and sulfate vary linearly with longitude across this region, reflecting the strong sources of these components of acid rain in the industrialized areas to the west. Particulate and gaseous components of nitrogen deposition (“dry deposition”) vary linearly with latitude, reflecting the shorter residence time in the atmosphere and the



**Figure 17.12.** Schematic diagram of the combination of a digital elevation model with station-level climate and deposition data to generate spatial estimates of the physical and chemical climate for the New England region, which can then be used to drive the PnET model. Based on Ollinger et al. 1993 and 1995, and Aber, Ollinger et al. 1995.



**Figure 17.13.** Regional patterns in daily levels of photosynthetically active radiation in July for the eastern United States. Modified from Aber and Freuder 2000, with permission from Inter-Research Science Publisher.

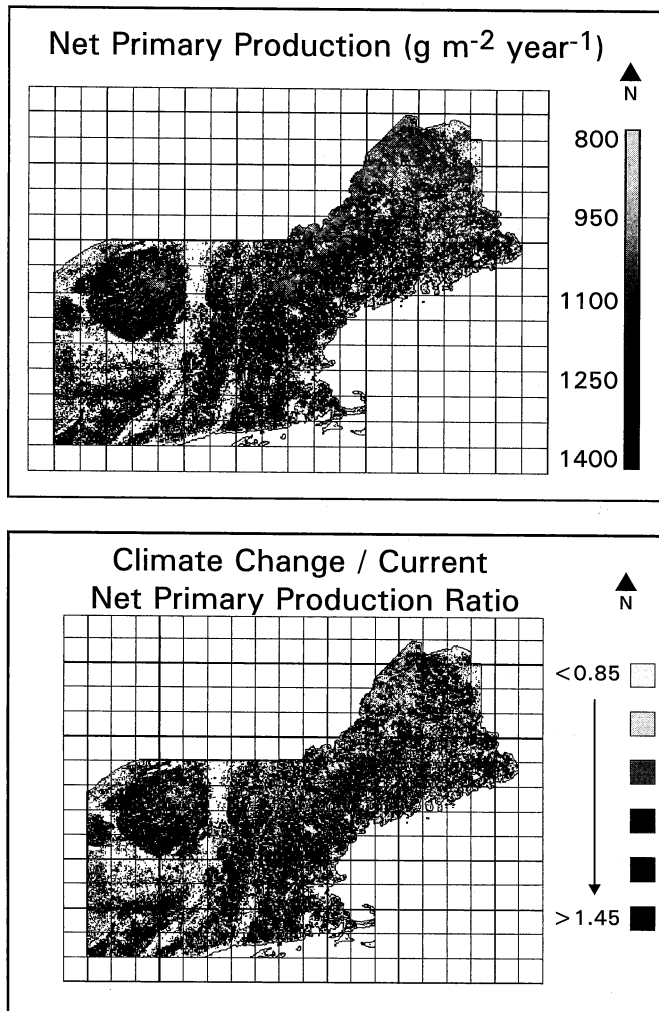
stronger sources along the heavily populated southern coast. Combining these trends provides a prediction of decreasing total nitrogen deposition from southwest to northeast across the region (Figure 17.12).

These spatial predictions of climate can be combined with maps of vegetation type to run PnET for every grid cell in the DEM (for example, in Figure 17.14, top, there are more than 300,000 forested “pixels”—roughly 1 kilometer in size—contained in the base map). In deciduous forests, productivity was strongly correlated with precipitation, suggesting that water limitations are important within this forest type. In contrast, for spruce-fir forests, productivity was most strongly related to annual growing degree days, indicative of the importance of length of growing season in these mostly high-elevation forests.

Model predictions can and should be tested at the regional scale as well as at the plot scale. We have compared PnET-II grid cell predictions of water yield (runoff to streams) with stream-flow measurements at thirty-four watersheds. Differences between predicted and observed

water yield averaged 6.0 centimeters per year, or about 8.4 percent of the mean water yield per site. Similar fractional differences between predicted and observed values for NPP were observed for eight stands for which detailed NPP values were available.

We also ran an initial test of the individual and combined effects of



**Figure 17.14.** Regional predictions from the PnET-II model for the current distribution of net primary production (NPP) based on estimated climate drivers and mapped forest-type distribution (top), and NPP as predicted under a scenario of elevated atmospheric CO<sub>2</sub> concentrations (2 × CO<sub>2</sub>) with a 6°C increase in temperature and a 15 percent decrease in precipitation (bottom). Bottom panel, modified from Aber, Ollinger et al. 1995, with permission from Inter-Research Science Publisher.

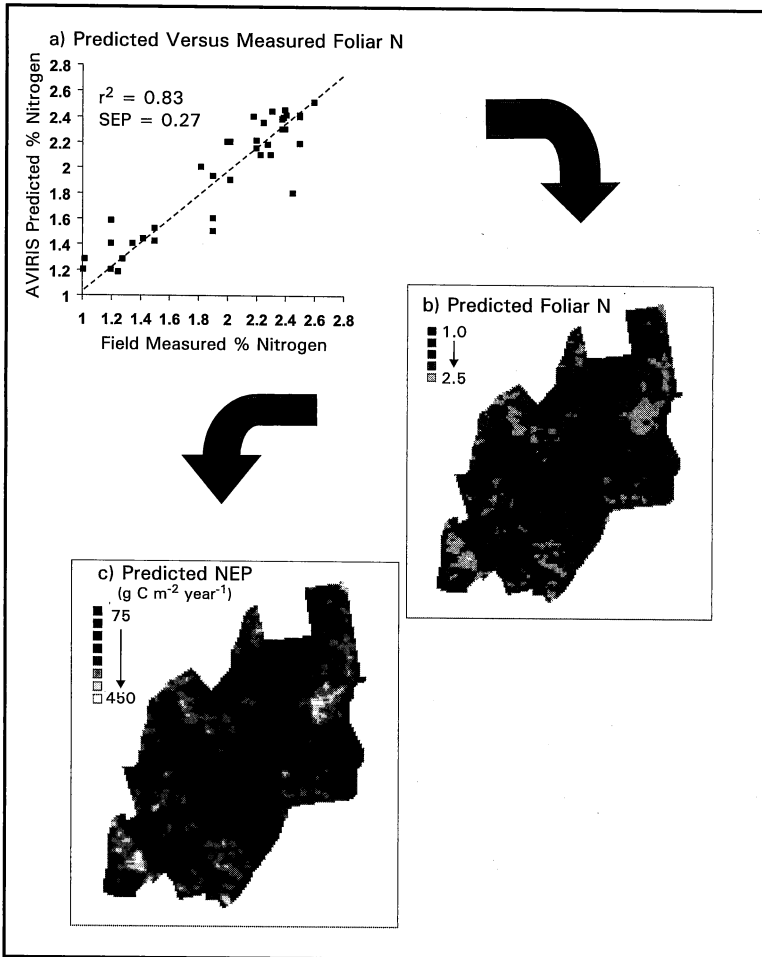
predicted changes in temperature, precipitation, and atmospheric CO<sub>2</sub> concentration. Using an early climate change scenario in which doubled CO<sub>2</sub> results in changes of +6°C and -15 percent precipitation, PnET-II predicts an increase in forest production (Figure 17.14, bottom) but a decrease in water yield, similar to values predicted for the Harvard Forest site alone. The more complete set of change scenarios analyzed with PnET-CN for Harvard Forest and Hubbard Brook has not yet been repeated at the regional scale.

### **The Link to Remote Sensing**

Our regional modeling efforts have been hampered by the lack of spatial data on some of the most important indicators of ecosystem function. Two of the most critical of these are characteristics of foliage: foliar nitrogen concentration, which is the most sensitive parameter controlling canopy photosynthesis, and foliar lignin and cellulose concentrations, which control decomposition in the DocMod model. These are whole-canopy parameters, and remote sensing is the only practical approach to measuring whole-canopy characteristics over large continuous areas. Early recognition of this problem led us to explore the potential for acquisition of basic model input parameters by remote sensing.

Traditional broadband sensors such as AVHRR (Advanced Very High Resolution Radiometer) and LANDSAT-TM (Thematic Mapper) do not provide enough spectral resolution (enough channels of information at the right wavelengths) to detect subtle changes in canopy chemistry. Instead, we have used a prototype sensor developed by the National Aeronautics and Space Administration (NASA) called AVIRIS (Airborne Visible Infrared Imaging Spectrometer), which provides 220 channels of information in the visible and near-infrared portions of the electromagnetic spectrum with approximately 10-nanometer spectral resolution. The instrument flies aboard a NASA ER-2 aircraft at an altitude of 70,000 feet, providing a spatial resolution on the ground of approximately 20 meters.

The high spectral resolution of the surface reflectance data provided by AVIRIS allows the application of laboratory-level spectrophotometric techniques for extraction of information. We have used first and second difference spectra (rates of change in reflectance across wavelength) in multiple linear regressions to calibrate equations predicting foliar nitrogen and lignin concentrations for a number of forest stands (for example, Figure 17.15), with accuracy approaching that of field measurements. We have used the data from the Harvard Forest as input to the PnET-II model and predicted spatial patterns of net carbon exchange for the Prospect Hill tract (Figure 17.15). The spatial average of these values

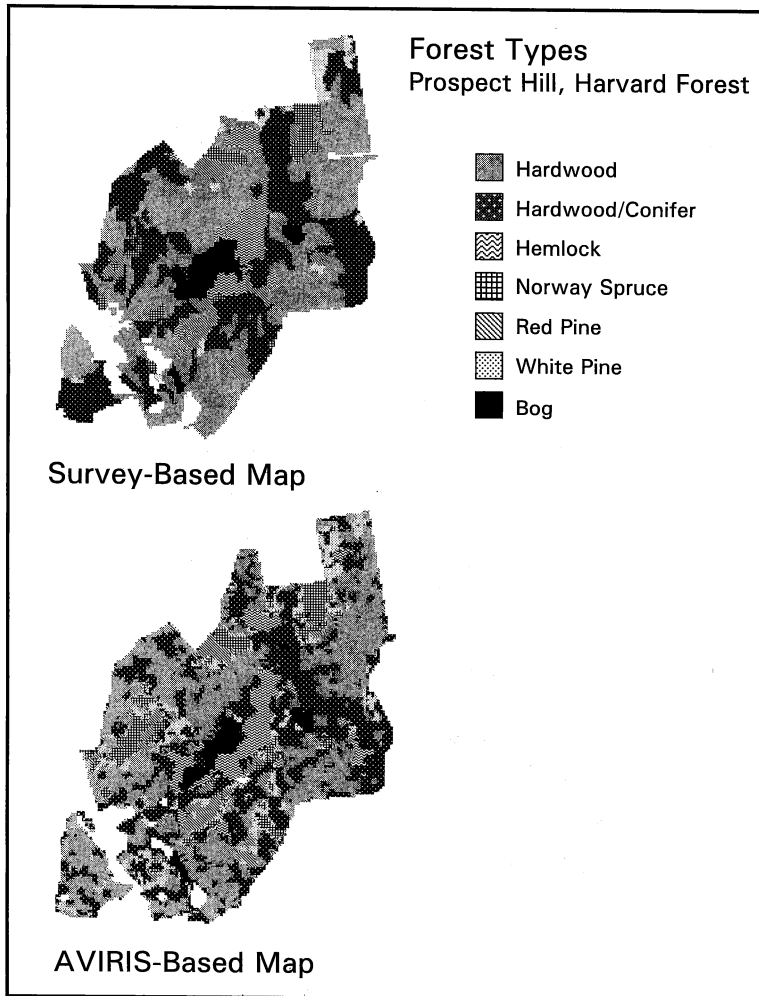


**Figure 17.15.** Use of high spectral resolution remote sensing (AVIRIS, airborne visible infrared imaging spectrometer) to derive whole-canopy foliar nitrogen concentration, used in turn as an input to the PnET-II model to estimate fine spatial scale patterns in net ecosystem production (NEP) for the Prospect Hill tract. a: A relationship between field-measured foliar nitrogen concentration and that predicted using AVIRIS; b: estimated foliar nitrogen for Prospect Hill; and c: PnET-II-estimated NEP. Modified from Martin and Aber 1997, with permission from the Ecological Society of America.

around the EMS tower is not inconsistent with the mean net ecosystem exchange estimates from the eddy covariance method.

AVIRIS data have also been valuable for refining maps of species distribution on Prospect Hill. Species vary in predictable and somewhat nonoverlapping ways with respect to the lignin and nitrogen concentra-





**Figure 17.16.** Distribution of forest types on the Prospect Hill tract of the Harvard Forest as mapped on the ground and as predicted from AVIRIS data. Note the identification of small areas of different species composition in the AVIRIS image that fall within larger areas mapped as large, heterogeneous units on the ground-based map. Modified from Martin et al. 1998, 252, with permission from Elsevier Science (copyright 1998).

tions in foliage. Using wavelengths that were appropriate for determining foliar chemistry, traditional supervised classification reproduced measured distributions of forest types and actually increased precision by delimiting pine and hardwood subcomponents within mixed stands (Figure 17.16). Separation at the species level was possible in pure stands (such as red pine versus white pine and spruce versus hemlock).