An Approach to Spatially Distributed Modeling of Net Primary Production (NPP) at the Landscape Scale and Its Application in Validation of EOS NPP Products

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Substantial research seeks to improve estimates of ecosystem processes and fluxes at a range of scales, notably from the stand scale (<1 km^2) using ecosystem physiology and eddy covariance techniques, to the landscape ($\sim10^2$ km^2) and global (10^8 km^2) scales using a variety of modeling and data acquisition approaches. One approach uses remotely sensed ecosystem properties in the scaling process. This approach combines digital maps of key ecosystem properties such as land cover type, leaf area index, and/or canopy chemistry with quantitative models of biological processes based on these ecosystem properties. Constraints on parametrizing models for global scale applications mean that relatively simple algorithms must be used which are based almost exclusively on satellite-derived inputs, for example, the planned Earth Observation System (EOS)-MODIS Land Science Team model output. Presently, there are limited ways of validating these outputs. At the landscape scale, the opportunity exists to combine remote sensing data with spatially distributed, process-based biogeochemistry models to examine variation in ecosystem processes such as NPP as a function of land cover type, canopy attributes, and/or location along environmental gradients. These process models can be validated against direct measurements made with eddy covariance flux towers and ground-based NPP sampling. Once run and validated over local landscapes, these fine scale models may provide our best opportunity to provide meaningful evaluation (or "validation" in some sense) of simpler, globally applied models. In this article, we 1) provide a biological framework that links ecosystem attributes and ecosystem carbon flux processes at a variety of scales, and summarizes the state of knowledge and models in these areas, 2) describe the need for developing NPP surfaces at a local landscape scale as a means of validating global models, in particular the MODIS NPP product, 3) describe the approach of the BigFoot project to performing such a validation exercise for a series of sites in North America, and 4) present an example using one such model (PnET-II) across diverse vegetation types in a heterogeneous landscape in central North America. ©Elsevier Science Inc., 1999

INTRODUCTION AND OBJECTIVES OF THE BigFoot PROJECT

Major uncertainties remain in measuring and modeling local, regional and global patterns of net carbon (C) exchange between the terrestrial biosphere and the atmosphere (Wofsy et al., 1993; Schimel, 1995; Aber et al., 1996; Baldocchi et al., 1996). Because of the broad spatial extents associated with regional- to global-scale efforts at modeling C flux, satellite remote sensing has often been employed to initialize, drive, or validate models. Considerable progress has been made in linking satellite imagery, derived products, and process-based net carbon exchange models at a variety of spatial scales; however, a number of research issues require attention. Notable among them is validation of carbon flux estimates over large domains.

Global scale modeling of net primary production (NPP) has been predominately done at large scales, that

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Table 1. Background Information on Initial BigFoot Study Sites

Site	Location	Major Cover Type	*Representative Leaf Area Index (m^2 m^{-2})*	*Representative Net Primary Production*	
				Above ground (MgC ha^{-1})	*Total (MgC ha^{-1})*
BOREAS	Thompson, Manitoba, Canada	Black spruce	4.2	1.2	2.2
Harvard Forest	Harvard Forest, MA	Mixed hardwood/conifer	4.7	4.0	7.0
Konza Prairie	Riley Co., KS	Tallgrass prairie	2.9	2.1	3.3
Reifsteck Farm	Urbana, IL	Corn/soybean	3.0	10.3	12.1

is, grids on the order of 50–250 km on a side (Esser, 1987; Mellilo et al., 1993). More recently, global scale modeling of NPP at the 1 km^2 resolution has been discussed (e.g., Prince and Goward, 1995) and is now planned in association with NASA's EOS Moderate Resolution Imaging Spectrometer (MODIS) Land Discipline Group (MODLAND). Planned to begin in 1999, MODLAND will estimate NPP using a light use efficiency approach with data from the MODIS sensor (see Running et al., 1999, this issue). This approach uses estimates of the absorbed photosynthetically active radiation (APAR) along with biome-specific efficiency factors (g C MJ^{-1}) derived from the process-based BIOME-BGC model (Running et al., 1994a; Justice et al., 1998). Both prior global model output (at much coarser resolution) and the planned MODLAND studies have potential scale-related spatial problems, and both the model output and the extent of such problems are difficult to validate and/or evaluate in meaningful ways.

Considering the wide range of approaches to modeling NPP, it is evident that the choices of grain size and model structure, although often selected for practical reasons, may seriously affect the accuracy of modeled NPP data. Multiple land cover types often exist even within a 1 km cell, and can have variable leaf area index (LAI), canopy chemistries, phenology, leaf structure, and production efficiencies. The degree to which an incongruency of vegetation patch size and model resolution is important for modeling NPP likely depends on how different the various observed vegetation patches within a 1 km cell are in terms of NPP, on the proportional distribution of patch types within the cell, and equally, on the degree of nonlinearity associated with the scaling of NPP to key ecosystem attributes.

Only limited attempts have been made at validating model-based C flux estimates even at a relatively modest landscape scale, such as 10^4 ha (Milner et al., 1996), let alone at larger scales (McNulty et al., 1994). There is often a fundamental mismatch in scale between the plot size of ground-based measurements of carbon flux and the size of the grid cells in large scale modeling efforts. Thus, stand-to-landscape scale estimates of net carbon cycling and NPP must be developed and validated which can then be compared to, and used to validate estimates made at larger, coarser, scales. That is the primary goal of the BigFoot Project.

BigFoot will use four or more sites covering a range of ecosystem types in North America including boreal and temperate forest, grassland, and crops (Table 1). At each site, process-based biogeochemistry models will be validated in the short-term against eddy covariance tower flux data and in the long-term against ground-based NPP data. These models will them be run in a spatially-distributed mode over a 2500 ha area and results will be compared to contemporaneous NPP estimates from MODLAND (Justice et al., 1998; Running et al., 1999, this issue). In this article the spatially distributed modeling aspects of the BigFoot project are described in relation to what is available (i.e., state-of-the-art) in terms of data, measurements, tools, and approaches, and to what constitutes validation of global-scale estimates such as MODLAND EOS products. As an example of the modeling approach, results are described from the application of one process-oriented model for estimation of NPP in a heterogeneous landscape at Cedar Creek, Minnesota, USA.

AVAILABLE DATA AND APPROACHES FROM REMOTE SENSING

Most models of NPP or net ecosystem exchange (NEE) are underlain by certain relatively simple biological principles, regardless of the way these are manifested in model calculations. Total annual carbon input to an ecosystem (annual gross primary production) is in fact a product of the size of the canopy (e.g., number of leaves× their size) multiplied by the average photosynthetic rate (e.g., productivity per unit leaf mass or area) during the proportion of the day and year when significantly greater than zero photosynthesis can occur. Clearly, accurate estimates of canopy properties and functioning as influenced by climate and local resource heterogeneity are needed in broad scale modeling efforts. Input variables relevant to canopy processes that can plausibly be derived from satellite imagery include land cover type (as influenced by natural factors as well as human use), leaf area index (LAI, the projected surface area of plant foliage), the fraction of incoming photosynthetically active radiation that is absorbed by the canopy (F_{APAR}), and other leaf structural and chemical attributes such as specific leaf area (SLA) and %N.

Land cover type is important because canopy properties or physiological rates often considered constants in models (such as LAI or maximum stomatal conductance or photosynthetic capacity) are sometimes based on assumed representative values for land cover types, and such values can vary widely among cover types (Reich et al., 1997). Satellite remote sensing has proved effective for the purpose of mapping cover types using either classification of multispectral data at a single point in time, for relatively small areas at fine spatial resolution (Bauer et al., 1994; Woodcock et al., 1994), or multitemporal data, for large areas at a relatively coarse spatial resolution (Loveland et al., 1991; Running et al., 1994b). The ability to resolve successional stages (Cohen et al., 1995), or effects of land use change (Moran et al., 1994), as well as simple biome type is an important consideration with respect to parametrizing C flux models.

Canopy N and SLA can be useful because they represent key leaf structural and chemical properties known to be related to leaf and canopy gas exchange rates (Reich et al., 1992; 1997; Gower et al., 1993; Landsberg and Gower, 1997). Efforts to map canopy nitrogen have been limited to high spectral resolution sensors such as AVRIS, and as yet results are not generalizable across sites or biomes (Martin and Aber, 1997). Information about SLA may be derivable indirectly from estimates of LAI since the two variables tend to be correlated across space within a particular biome (Pierce et al., 1994). In both cases a great deal of continued research is needed before operational retrieval from satellite imagery is feasible.

LAI is desirable for C flux and NPP modeling because of its strong influence on canopy energy balance and rates of gas exchange. LAI over large areas is hypothesized to be obtainable from empirical relationships of LAI measured in the field to spectral vegetation indices (SVIs) derived from satellite image data (Begue, 1993; Spanner et al., 1994), although there are serious problems to be overcome. At low LAI, the influence of reflection from uncovered ground must be accounted for (van Leeuwen and Huete, 1996) and the preponderance of evidence is that SVIs (in particular, NDVI and the SR) are generally asymptotic with respect to LAI (Fassnacht et al., 1997; Turner et al., 1999, this issue). Nevertheless, both empirical relationships and more complex algorithms employing radiation transfer models have strong potential for retrieving LAI from remote sensing imagery over large domains. F_{APAR} is more linearly related to NDVI than is LAI, so that retrieval using remote sensing is less problematical (Ruimy et al., 1994).

The challenges of modeling C flux or NPP from LAI and deriving accurate estimates of LAI from relationships with image SVIs have aspects in common. There tends to be a close relationship of NPP to LAI at relatively low LAIs; however, once a certain level of canopy cover and LAI is reached, increasing above-ground NPP (ANPP) becomes less tightly related to LAI or canopy mass (Waring, 1983; Reich et al., 1992; Landsberg and Gower, 1997). The physical basis for why NDVI, SR, and ANPP are nonlinearly related to LAI is well understood, as is why the relationships are asymptotic. In essence, as canopies get denser, additional increases in light interception decline toward zero; and thus both remote measures such as NDVI and SR, and biological processes such as canopy CO_2 assimilation also increase less and less. Several simulation approaches have been suggested that all in some fashion quantify the relative efficiency of a canopy of a given size at assimilating carbon out of the atmosphere. These approaches are based on combining the physiological attributes of the foliage with the canopy size and arrangement and directly or indirectly estimating the efficiency with which intercepted light is utilized (Running et al., 1994a; Field et al., 1995; Aber et al., 1996; Landsberg and Waring, 1997).

Measurements of radiation utilization efficiency (ε) have indicated considerable variation (see Gower et al., 1999, this issue). There is evidently a tradeoff (among species) between LAI (and especially canopy mass) and the production efficiency and photosynthetic physiology of foliage (Reich et al., 1992; 1994a; Gower et al., 1993). Species with high LAI or canopy foliage mass tend to have low SLA and therefore low NPP per unit LAI or leaf mass due to low maximum photosynthetic rates coupled with increased shading (Reich et al., 1992) (Fig. 1). This biological heterogeneity is responsible in part for the wide range of reported radiation utilization efficiencies, which complicate the process of modeling NPP based on an absorbed radiation approach (Running et al., 1994a; Field et al., 1995; Landsberg and Waring, 1997). It is also likely that radiation utilization efficiency is (at least partially) independently a function of climate. Thus, although LAI and F_{APAR} provide substantial information, there are complications that must be addressed.

How Can Global Scale Models Dependent on Satellite Imagery Be Evaluated?

There are presently limited means for evaluating regionally or globally applied C flux models. Comparisons to C sources and sinks inferred from inverse modeling of the global C cycle, which is based on spatial and temporal variation in the atmospheric CO_2 concentration (e.g., Fan et al., 1998), has been used in some cases (Hunt et al., 1996; Denning et al., 1996). Other attempts have involved intermodel comparisons (VEMAP, 1995). In thinking about how to better evaluate, or hopefully someday validate, global-scale models, such as the MODLAND NPP algorithm, it is important to consider the strengths, weaknesses, and scales of various direct and indirect (i.e., modeling) approaches. This is so important that we will revisit the basic concepts involved in carbon flux dynamics, to define what part of the biosphere–atmosphere carbon exchange is of interest and how we are able (or in many cases unable) to effectively measure or model these fluxes.

For global carbon balance considerations, net eco-

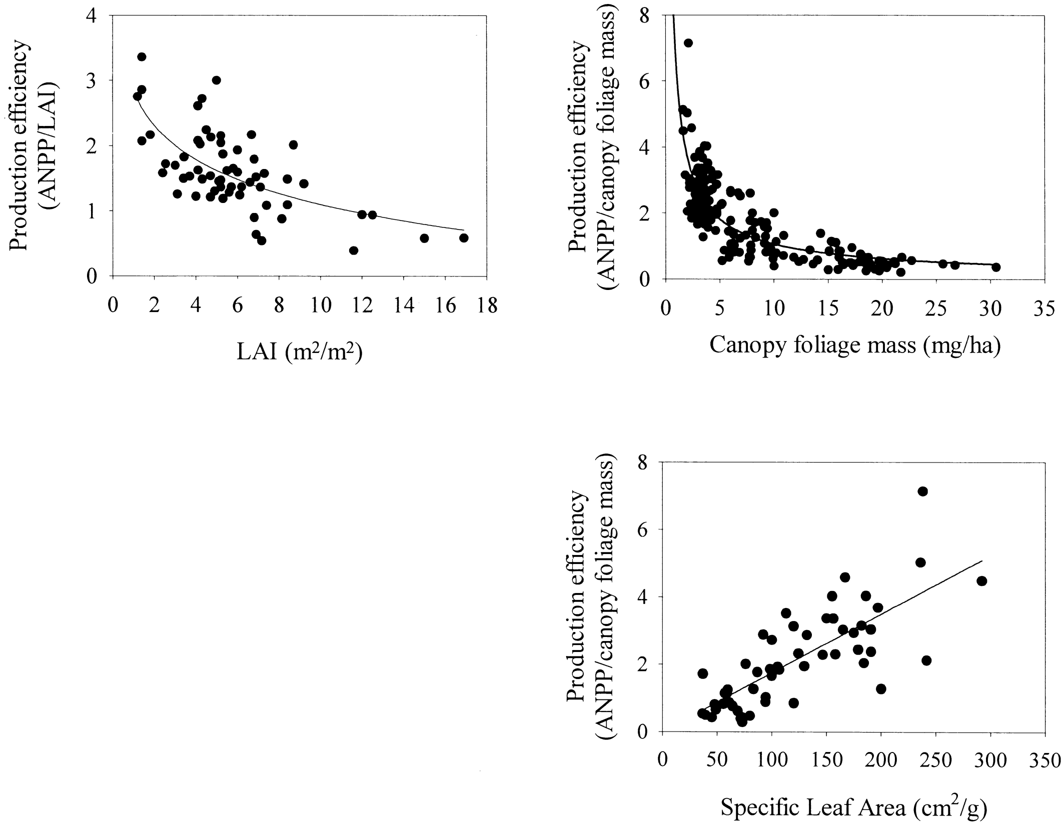

Figure 1. Forest canopy production efficiency (ANPP per unit canopy foliage mass or LAI) in relation to several canopy measures: (upper left) relationship between production efficiency (LAI basis) and LAI, data from Reich (1998) plus Fassnacht and Gower (1997), $\log_{10}(\mathrm{ANPP/LAI}) = 0.42 - 0.0427{*}\mathrm{LAI}$, $r^2 = 0.49$, $n = 60$; (upper right) relationship between production efficiency (foliage mass basis) and canopy foliage mass, data from Reich (1998), $\log_{10}(\mathrm{ANPP/canopy\ foliage\ mass}) = 0.84 - 0.878{*}\log_{10}(\mathrm{foliage\ mass})$, $r^2 = 0.75$, $n = 178$; and (lower right) relationship between production efficiency (mass basis) and specific leaf area on a projected basis, data from Reich et al. (1997) and Reich (1998), $\mathrm{ANPP/canopy\ foliage\ mass} = -0.04 + 0.01776{*}\mathrm{SLA}$, $r^2 = 0.59$, $n = 54$.

system exchange (NEE) of CO_2 is of great interest. NEE is defined as the net carbon dioxide flux to or from an ecosystem, and integrates all ecosystem carbon sources and sinks: $\mathrm{NEE} = \mathrm{GPP} - R_a - R_h$, where GPP is gross primary production (i.e., total gross photosynthesis), R_a is autotrophic respiration, and R_h is heterotrophic respiration. Total net primary productivity considers only the autotrophic part of the ecosystem (i.e., $\mathrm{NPP} = \mathrm{GPP} - R_a$) and is of equal but different importance globally than NEE, given our dependence on NPP for all of our food, fiber (wood, etc.) and many other ecological and agricultural services. Annual NPP can also generally be estimated by: $\mathrm{NPP} = \Delta B + \mathrm{tissue\ turnover} + \mathrm{herbivory}$, where ΔB is the change in the autotrophic biomass pool and tissue turnover includes above-ground litterfall and below-ground fine root turnover. Although these concepts are simple, no one technique provides accurate measurements of all of these carbon fluxes at even one spatial or temporal scale, making NPP and NEE model validation surprisingly difficult.

The eddy covariance flux approach is attracting increasing interest for monitoring of NEE (e.g., the Fluxnet and Ameriflux Networks). Measurement of ecosystem scale gas fluxes integrated over the area of the tower "footprint" (~1 km^2) can provide information about the functioning of ecosystems, and are of potential use as validation data for other larger scale efforts. NEE can be estimated directly but the measurement requires heavily instrumented eddy covariance flux towers, ideally located in flat terrain and in large homogeneous patches of vegetation, and relies on a number of assumptions that may frequently be violated. Eddy covariance-based NEE estimates are thus a kind of model output although this is only infrequently recognized. Nonetheless, eddy covariance flux towers are by far the best available direct means of estimating NEE. Additionally, eddy covariance data can be used to provide estimates of GPP and Rt (ecosystem respiration, $R_a + R_h$) , but provide no means of estimating NPP.

The relationship of nighttime NEE (which is nighttime $R_a + R_h$) and nighttime temperature can be used with daytime temperature to estimate daytime $R_a + R_h$, and hence GPP (i.e., GPP=daytime [NEE+R_a+R_h]) (e.g., Aber et al., 1996). However, since there is no way of separating R_a from R_h using this technique, it is impossible to estimate. To estimate NPP using eddy covariance data, therefore, one must rely on modeling in order to separate R_a from R_h. Unfortunately, of all processes modeled with biogeochemistry-type models, separate estimates of microbial and root respiration have proved among the most intractable. The situation becomes even more problematic if eddy flux data are used to estimate above-ground NPP (ANPP), since there is no way of partitioning NPP to above-ground vs. below-ground components except by highly arbitrary modeling assumptions in most cases. Thus, eddy covariance techniques by themselves provide us with the best available estimate of NEE and probably the best if an indirect estimate of GPP, but a poor means of estimating NPP or ANPP. In contrast, MODLAND or other globally applied models are likely to be able to estimate ANPP relatively well, NPP to a lesser degree, and NEE even more problematically. As discussed below, there is also a mismatch in spatial scale between the footprint of eddy flux measures and the size of grid cells in most global models, and, given the costs involved, it is unlikely that a sufficiently large eddy flux network could ever be developed to be of much use as a direct comparison for global models.

NPP, or its subcomponent ANPP, is technically simpler to measure than NEE, and thus data are available for far more sites. However, because of the difficulty in accurately measuring or modeling below-ground NPP, accurate estimates of total NPP are, perhaps surprisingly to nonspecialists, still extremely scarce (Gower et al., 1994) and both difficult and expensive to obtain. In contrast, ANPP is considerably easier to measure than below-ground (and hence total) NPP, and far more is known about ANPP than total NPP. Therefore, validation of satellite-based C flux estimates or any coarse-scaled carbon balance model, especially at multiple sites, will be more feasible if the measure initially used is ANPP rather than NPP or NEE. It is important to note, however, that most measures of ANPP are likely not even particularly accurate (few attempts to assess their accuracy have been made so it is difficult to say precisely). Given that the approach is decidedly "low-tech" and has been available for decades, this also may be surprising to some readers. However, most estimates of ANPP in either forests or herbaceous vegetation types are dependent on a number of assumptions, often involving turnover rates, which are likely violated frequently; and most estimates of ANPP suffer from "undersampling" as well.

A key point here is the fundamental mismatch in temporal and spatial scale and patchiness between global model outputs and direct observations. The spatial resolution of the EOS MODLAND NPP products will be 1 km^2, and the grid cells for many globally applied models are considerably larger. Traditional ground-based measures of ANPP are possible for tens of individual plots, each quite small (0.000025–0.0025 km^2 scale is typical), but cost and difficulty preclude measuring below-ground NPP (and hence total NPP) for more than one or two very small plots within 1 km^2. Moreover, in the temperate zone the time scale for such measurements is effectively 1 year, and the plots used to characterize any given 1 km^2 cell will not necessarily reflect the true conditions over the entire cell. Thus, plot-level measurements alone have substantial problems as a method for MODLAND validation, including: a mismatch of spatial scales; an opposite mismatch of temporal scales; lack of representativeness of the entire landscape; and relatively low data replication.

Eddy covariance flux measurements provide a larger (but variable) footprint and a direct measure of NEE over a wide range of temporal scales. However, as mentioned above, eddy covariance flux measurements do not provide NPP estimates and the modeling required to do so is at present far less feasible than most other types of ecosystem modeling. Moreover, a very low number of eddy flux tower sites will ever be available at any spatial scale. Thus, eddy covariance measurements also have substantial problems as a vehicle for MODLAND validation, including 1) no direct means of estimating NPP, 2) lack of representativeness of the entire landscape, and 3) very low data replication.

To summarize, eddy covariance techniques provide our best estimates of NEE whereas direct plot-level sampling provides our best estimates of NPP (Gower et al., 1999, this issue). The inadequacies with both types of measurements, and with the related global data bases, are indicated here not out of negativity, but in an attempt to reveal the difficulties in developing an effective approach to evaluating global scale models. In contrast, by validating biogeochemistry models against ground-based NPP data and eddy covariance GPP data, and by then applying these spatially distributed biogeochemistry models over a domain (25 km^2) which includes multiple MODIS pixels and at a spatial resolution (25 m×25 m) which is relevant to NPP measurements, BigFoot should provide a basis for comparison with satellite-based global NPP products such as MODLAND output at sites representing several of the major biomes. It is logical and likely (but not certain) that the BigFoot output should be more accurate than the MODLAND output, and thus it is fair to call this a validation or "validation exercise" (as one prefers). In any case the errors in the BigFoot NPP surfaces will be well characterized by reference to flux tower daily time step GPP measurements and plot-level, annual time step NPP measurements (Gower et al., 1999, this issue) dispersed over each 25 km^2 site. In the remainder of this article we will describe how spatially explicit, process-based NPP models may be validated against eddy flux and ground-based NPP data and subsequently be applied at the landscape scale where in turn their output may be useful in evaluating ("validating") satellite-based global NPP products.

MODEL SELECTION, APPLICATION, AND VALIDATION FOR BigFoot

An enormous range of complexity exists in current models that estimate NPP and related carbon cycling components. At the most mechanistic end of the continuum in model complexity are hourly time step models which highly disaggregate plant components and treat processes based on fundamental physical, biochemical, and physiological principles. Input requirements are extensive and the optimal methods for validation include eddy correlation flux data and ancillary gas exchange measurements. At the other end of the continuum are simplified radiation-based approaches, as will be used by MODLAND, in which the focus is on quantifying absorbed photosynthetically active radiation and applying it to an appropriate generalized light use efficiency factor. Several variants of this approach have been examined, and it has been shown to have promise in more localized studies (McMurtrie, 1991; Prince and Goward, 1995; Waring et al., 1995; Landsberg and Waring, 1997). A critical problem at the regional or global scale is accurately assigning a light use efficiency to different vegetation types under different climates and seasons (Ruimy et al., 1994; Landsberg and Gower, 1997). Between the extremes are NPP models in which plant structure and processes are aggregated to some degree relative to the highly mechanistic models but whose input requirements are such that the models can be still be applied in a spatially-distributed mode (e.g., VEMAP, 1995).

For the purposes of developing NPP surfaces for areas on the order of landscapes to regions, it is these models of intermediate complexity which may hold the most promise (Running et al., 1999, this issue). The least demanding of this class of models are those which require only climatic driving variables (often at a monthly time step) and vegetation type (e.g., Esser, 1987; Mellilo et al., 1993). These models have typically been developed for simulation of changes in NPP in response to environmental change. Models which also require LAI (potentially derived from remote sensing) tend to be more physiologically based and have application for monitoring current NPP (e.g., Running and Hunt, 1993). In both approaches, the computational requirements for the models over an annual cycle on grids up to 10^5 cells are within the capabilities of contemporary workstations.

Besides problems associated with model complexity and the number of inputs, NPP modeling projects must also address the issue of the optimal spatial resolution of the analysis. Running a process-based NPP model for a year or more at the 25 m resolution over the $\sim 149 \times 10^6$ km^2 terrestrial surface is not computationally feasible. Nevertheless, there is significant spatial heterogeneity relevant to carbon flux modeling induced by human land use at relatively fine spatial resolutions. Several studies have documented potential for errors in NPP estimates associated with coarsening the spatial resolution of the analysis (White and Running, 1994; Turner et al., 1996). Thus there will usually be a compromise between spatial resolution and spatial domain such that alternative modeling approaches are required as the domain of interest increases.

Given the constraints and goals of the BigFoot project, two NPP models of intermediate complexity are being used which have been applied broadly and validated in at least several instances: Forest-BGC/BIOME-BGC (Hunt and Running, 1992; Running and Hunt, 1993; Running, 1994; Hunt et al., 1996) and PnET (Aber and Federer, 1992; Aber et al., 1995; 1996). For instance, Forest-BGC estimates of ANPP were compared to measured ANPP for sites across the Oregon transect, and PnET estimates of ANPP were originally (1992) compared to measured ANPP values for a variety of forested sites. Both Forest-BGC and PnET originated as process-based forest ecosystem models, but have designs that allow modification for other vegetation types such as grasslands (see below).

The use of PnET will provide independent values for comparison with MODLAND output, and thus is of critical importance in this exercise. BIOME-BGC cannot be considered to provide independent output relative to MODLAND products because it is used in the MODLAND NPP model algorithm for estimation of epsilon (Running et al., 1994a; Justice et al., 1998). However, use of BIOME-BGC at the landscape scale will permit investigation into the role of factors such as spatial resolution, land cover classification scheme, and alternative values of epsilon in the differences between the global NPP products and the local BigFoot NPP products.

The principles underlying the canopy model of PnET include fundamental physiological relationships (and constraints on their combinations) between climate, photosynthetic capacity, ecosystem leaf mass and area (LAI) per ha, and leaf longevity (Reich et al., 1992; 1994a; Gower et al., 1993). Canopy size does not usually vary independently of foliage attributes. For instance, across the diverse Oregon transect and comparing closed canopy forests, there are strong relationships between LAI and leaf traits such as SLA. However, these relationships can be opposite in direction, depending on whether variation in properties is largely driven by climate (as across the Oregon Transect) or by species differences. Across a strong precipitation gradient where canopies are larger under moister conditions, leaves have higher SLA (Pierce et al., 1994) because of the general relationship of SLA to site moisture conditions (Reich et al., 1999). In contrast, for closed canopy forests of all kinds (in a comparison where the majority of variance was due to forest type rather than climate), canopies can either be relatively sparse (low LAI or canopy leaf mass) but with highly productive leaves (high photosynthetic capacity) or dense (high LAI or canopy leaf mass) with low productivity leaves (low photosynthetic capacity) (Gower et al., 1993; Reich et al., 1992; 1994a; 1997). As a result of these patterns, opposite gradients of canopy production efficiency (which should scale closely with radiation use efficiency) exist: In one case (across a climate gradient) productivity per leaf increases with canopy size, and in the other case (across forest types within closed-canopy forest types) productivity per leaf decreases with canopy size. Having a better ability to quantify these relationships (of leaf traits to canopy traits) across all sources of variation will be critical to continuing development of effective generalized models.

The canopy productivity subroutine of PnET is based on the differential relationship between photosynthetic capacity, leaf dark respiration, and leaf nitrogen for differing plant functional types (Reich et al., 1994b; 1995; 1998a,b) and on the scaling of leaf structure and function vertically through a canopy (e.g., Ellsworth and Reich, 1993).

The photosynthesis leaf N subroutine of a 1995 eastern deciduous forest model version of PnET was developed from data for trees of central North America, and the model was successful in predicting canopy net photosynthesis when compared to eddy flux data for Harvard Forest in Massachusetts in eastern North America (Aber et al., 1996). For the BigFoot application, the leaf photosynthesis and respiration parameters (maximum photosynthetic rate and basal foliar respiration rate) for PnET will be estimated as a function of leaf %N and SLA, based on process oriented relationships that vary for different functional types and biomes (Reich et al., 1998a,b; 1999), replacing more limited algorithms used earlier (Aber et al., 1996). PnET has a relatively modest list of required input variables, the most important of which are LAI, leaf %N, canopy phenology, soil water-holding capacity, air temperature, and precipitation.

BIOME-BGC has a daily time step for key processes in the hydrologic cycle (precipitation, interception, transpiration, snow melt, and runoff) and carbon cycle (photosynthesis and maintenance respiration). Transpiration is estimated using the Penman Monteith equation and thus is sensitive to radiation and vapor pressure deficit. The carbon assimilation algorithms are from the model of Farquhar et al. (1980). Maintenance respiration is determined by biomass, tissue N concentration, a base rate, and a Q_{10}. Recent enhancements include an internal leaf phenology related to air temperature, a subannual carbon allocation scheme, and a decomposition module. BIOME-BGC has been run globally at a coarse resolution (Hunt et al., 1996). The input requirements for Biome-BGC are similar to PnET, with the additional need for daily solar radiation (Hunt et al., 1996).

Modeling C flux or ANPP on a landscape scale at a 25 m grain size offers numerous challenges, even after estimates of land-cover class (Thomlinson et al., 1999, this issue) and LAI (Turner et al., 1999, this issue) have been developed. Percent N, SLA, soil water-holding capacity, and climate are some of the key input variables which vary spatially and/or among land-cover classes and will need to be estimated in BigFoot across the four or more sites. Several of the variables will be estimated as a function of land cover class or a combination of cover and LAI (canopy light attenuation, foliar %N, SLA). Alternative sources for initializing these variables will be the field data collected in this study and existing global scaling relationships developed for vegetation in various biomes (Reich et al., 1992; 1995; 1997; 1998a,b; Aber and Federer, 1992; Aber et al., 1996; Hunt et al., 1996).

Climatic variables, including solar radiation, temperature, precipitation, and humidity are critical inputs to the NPP models. Each of the four planned BigFoot sites has relevant climate data for one to several points from site meteorological stations. The meteorological data can be readily interpolated across the landscape based on a digital elevation model and algorithms such as MTCLM (Running et al., 1987). The issue of juxtaposing NPP measurements with time-series climate data for the same year or interval is important because of significant interannual variation in climate evident at most of the sites. In the case of forests, where estimates of bole production will be based on radial increment determined from tree cores, growth is estimated over a period of 5 or more years and the relevance of the long-term average climate is obvious. In biomes, such as a grassland, where annual ANPP is more closely tied to the climate of a given year, attention to the difference between the year of ANPP measurements and the long-term average climate is more important.

Validation of the GPP model component of the NPP models to be used in BigFoot will be made by comparing their outputs to estimates from eddy flux measurements at each site, as done for temperate forests by Waring et al. (1995) and Aber et al. (1996). One of the exercises done in temperate forest at Harvard Forest (Aber et al., 1996) provides a useful example. PnET was run on a daily time step (PnET-Day) to enable close comparison of simulated GPP to the GPP estimated with eddy flux data. Agreement between PnET-DAY and tower data was generally very good (Fig. 2). Comparisons of monthly aggregated tower data were made with model runs at decreasing levels of specificity. PnET was either 1) run daily using tower weather data and averaged per month, 2) run for 1 day using the monthly average of the tower climate drivers (and multiplied by the number of days in the month), or 3) run for the average day of the month using mean monthly climate data from off-site. The three aggregation methods produced similar results and average daily GPP for the 4-year period ranged from 3.9 to 4.3 g C

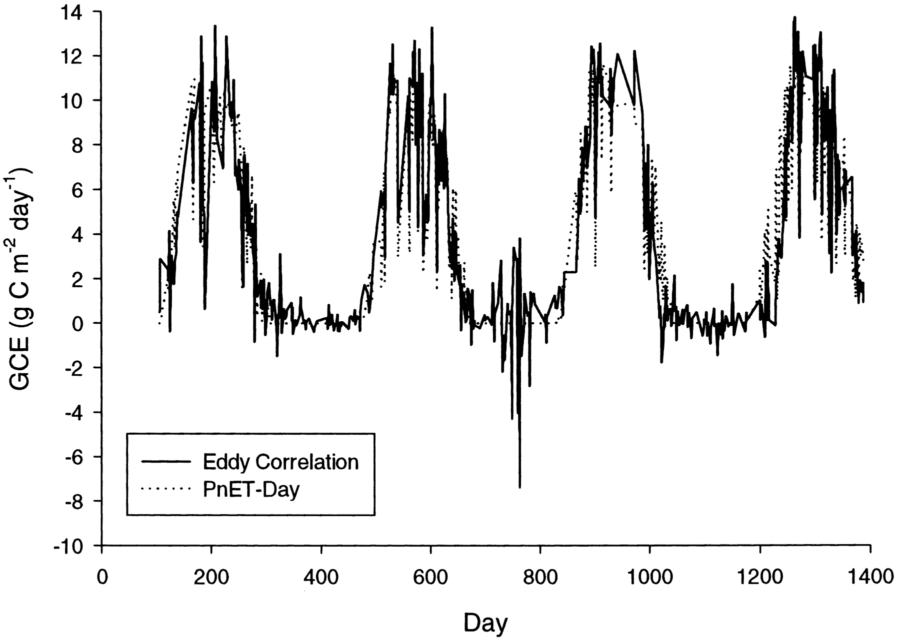

Figure 2. Comparison of temporal patterns (1991–1994) in simulated gross carbon exchange, GCE (equivalent to GPP in this article) predicted by the PnET-Day model and measured using eddy correlation at Harvard Forest. Day 1 is 1 January 1991. From Aber et al. (1996).

m^2/d for the three aggregation methods. Such results suggest that accurate predictions of monthly GPP can be obtained using monthly mean data from off-site sources or models at this eastern hardwood forest site. In coniferous forests of the western United States where site water balance is more critical, a daily or weekly time step may be required to adequately model GPP.

Validation of the annual NPP model components will be made at each site by comparing their output to direct measurements of NPP (above- and below-ground) made at the flux tower and measured ANPPs made at 25–30 other plots dispersed over the 25 km^2 study area (Gower et al., 1999, this issue). Each study area will be initially stratified on the basis of remote sensing-based land cover classification scheme, with additional stratification by factors such as soils, slope, and aspect if needed. Model accuracy can then be characterized within each cover type, across all cover types within a site, and across all sites treated by BigFoot.

A key theme in NPP model runs will be testing the generality of the model algorithms and associated “constants.” For example, the accuracy of model output (for all sites) based on runs made without site-specific leaf N values will be compared to the accuracy based on model runs made with site-specific leaf N values. The close coordination of leaf and canopy SLA, %N, total foliage mass and LAI, photosynthetic capacity, and leaf life span observed in nature (Reich et al., 1992; 1997, Gower et al., 1993) and incorporated in the logic of PnET (Aber et al., 1995; 1996) will potentially result in generic models functioning almost as well as models with substantial site specific information. It is important to test these issues in this study, given that modeling of NPP over large areas, and for parts of the world where little ground data are available, will require generic models.

EXAMPLE OF PnET APPLIED IN A HETEROGENEOUS LANDSCAPE

PnET and BIOME-BGC were developed based on concepts of upland forest ecosystem functioning, and it is not yet clear how easily or well those concepts can be modified for application in different ecosystems. Modeling in diverse landscapes may include canopies which are much sparser and patchier (e.g., savannas), vegetation types that do not have woody perennial tissue (e.g., grasslands), vegetation types with dissimilar plant–soil interactions (marshes and forested wetlands), or annual vegetation types (agricultural ecosystems). The heterogeneous landscape in and around the Cedar Creek Natural History Area in east central Minnesota contains such elements, and many of the BigFoot sites will contain a similar range (if different type) of heterogeneity.

As one of the initial stages of the BigFoot project, a 30 km^2 land cover map of Cedar Creek (Fig. 3) was developed and PnET was parametrized for 10 different vegetation types (land cover classes) for which some validation NPP data were also obtained. Color infrared aerial photographs were acquired in October 1994. These were photointerpreted by an ecologist familiar with the study area and vegetation of the region. Control locations were measured using a global positioning system receiver, and interpreted vegetation boundaries digitized and registered to a known coordinate system using these control points. These data were then rasterized to various cell sizes, using a modal assignment rule. The land-

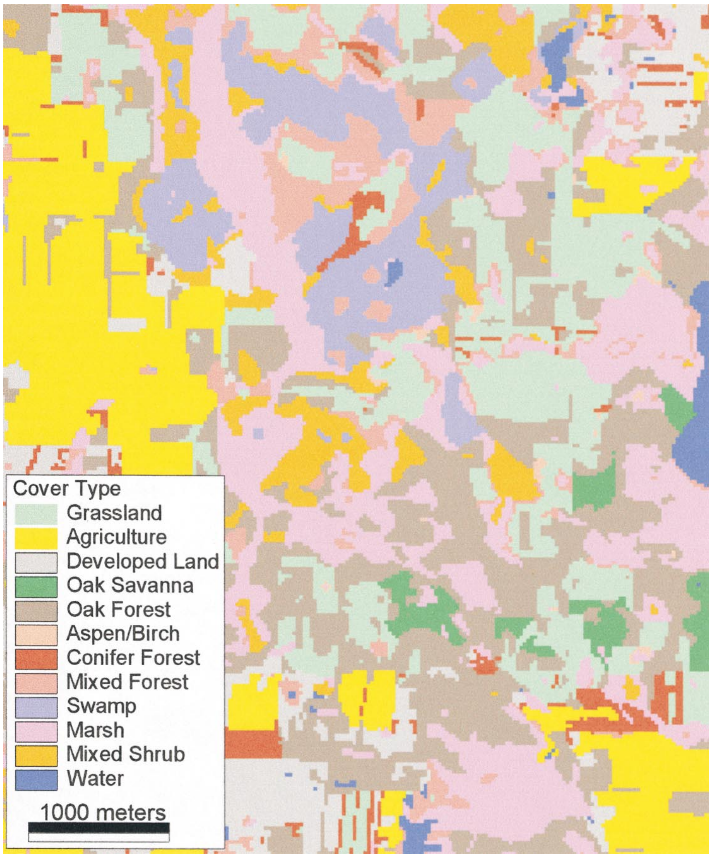

Figure 3. Land cover class map for a 6 km×5 km area surrounding Cedar Creek Natural History Area, in east central Minnesota, USA.

cover class (LCC) map so developed originally contained 34 vegetation types, but these were collapsed into 10 classes, because this was the largest number for which model parameters could be reasonably provided. Alternatively, several vegetation types for which the model could be parametrized (different subclasses of oak woodlands and savannas, or corn vs. soybean crops, etc.) were not differentiable in the LCC process, and so were lumped here.

Several parameters of PnET varied among land cover classes. These included: the algorithms for the photosynthesis–N relationship (Reich et al., 1997; 1998a; 1999) and the values of leaf %N, SLA, and maximum and minimum foliage mass (and hence LAI), C allocation algorithms, and soil water-holding capacity. Input parameters such as %N, SLA, LAI, and carbon allocation fractions were determined based on field sampling, as will be the case in BigFoot. Data from a local weather station for a typical year were used in running the model.

Total annual ANPP simulated by the model compared relatively well with direct observations (Reich and Bolstad, in preparation). Estimates from PnET for all LCCs were within 10% of the mean of directly measured ANPP for plots within each LCC (data not shown). Simulated ANPP was highest in agricultural and marsh vegetation, intermediate in most forested land, and lowest in old field grasslands. It is especially interesting that crop, grassland, and forest stands with canopy sizes not altogether different display large differences in simulated nonfoliar production that are consistent with direct observations and with differences in potential photosynthetic performance of leaves of these different functional types. For instance, crops (mix of corn and soybean) had a relatively low LAI, yet a high potential photosynthetic rate combined with a high priority of allocation to reproduction yielded a high ANPP in the model, similar to the direct observation.

Both LCC and ANPP were initially mapped at a 25 m grid cell size (Fig. 4). The potential effects of aggregation were also investigated by mapping LCC and ANPP at different grid cell sizes (250 m, 500 m, and 1000 m). For each aggregation the LCC for each cell was defined as being that of the dominant (modal) LCC, and the mean ANPP for that LCC was assigned to that cell. The average ANPP for the entire 3000 ha area was 8.97 Mg ha^{-1} yr^{-1} based on the finest scale aggregation (25 m cell size). Aggregation at the 250 m and 500 m cell sizes yielded total ANPP estimates for the 30 km^2 area that were within 1% of the fine scale estimate. However, the 1-km-scale estimate (9.43 Mg ha^{-1} yr^{-1}) was 5% different. An LCC that was patchily distributed across the landscape would probably "disappear" during a coarsening aggregation process, with proportionate impacts on total ANPP. Alternatively, an LCC which is clumped would likely tend to dominate aggregated cells and might

Figure 4. Above-ground net primary productivity (ANPP) class map for a 6 km×5 km area surrounding Cedar Creek Natural History Area, in east central Minnesota, USA, at four spatial aggregations. For each map, land cover class of each grid cell was characterized as belonging to dominant (plurality) class, and assigned ANPP values for that LCC based on a biogeochemistry process model (PnET-II) that was run for each LCC.

become more important at a coarse scale, as was the case for agricultural land in this exercise—it represented 15% of the area of the 25-m cells, but was 20% of the area at the 1-km grain size. Other studies (e.g., M. Turner et al., 1989; Pierce and Running, 1995; D. Turner et al., 1996) have similarly found significant relationships between patterns in land cover heterogeneity and the effects of varying the spatial resolution in an analysis.

SUMMARY

Constraints on parametrizing global-scale carbon flux models suggest that most such efforts will use relatively simple algorithms based primarily on satellite-derived inputs, such as the planned Earth Observation System (EOS)-MODIS Land Science Team model output. At present, the capacity to validate such models is limited. At a finer landscape scale, spatially distributed, process-based biogeochemistry models can be used to examine variation in ecosystem processes such as NPP as a function of land cover type, canopy attributes, and/or location along environmental gradients. These process models can be validated against direct measurements made with eddy covariance flux towers and ground-based NPP sampling. Once run and validated at local landscape scales, these fine scale models may provide our best opportunity to "validate" simpler global models.

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