

Integrating Remote Sensing and Ecosystem Process Models for Landscape- to Regional-Scale Analysis of the Carbon Cycle

DAVID P. TURNER, SCOTT V. OLLINGER, AND JOHN S. KIMBALL

A growing body of research has demonstrated the complementary nature of remote sensing and ecosystem modeling in studies of terrestrial carbon cycling. Whereas remote sensing instruments are designed to capture spatially continuous information on the reflectance properties of landscape and vegetation, models focus on the underlying biogeochemical processes that regulate carbon transformation, often over longer temporal scales. Remote sensing capabilities, developed over the past several decades, now provide regular, high-resolution (10-meter to 1-kilometer) mapping and monitoring of land surface characteristics relevant to modeling, including vegetation type, biomass, stand age class, phenology, leaf area index, and tree height. Integration of these data sets with ecosystem process models and distributed climate data provides a means for regional assessment of carbon fluxes and analysis of the underlying processes affecting them. Applications include monitoring of carbon pools and flux in response to the United Nations Framework Convention on Climate Change.

Keywords: remote sensing, models, carbon flux, landscape, regional

The array of airborne and satellite sensors deployed to monitor the biosphere has increased rapidly over the last decade (Lefsky and Cohen 2003). Land cover can be readily mapped at a variety of spatial resolutions and degrees of disaggregation, and biophysical state variables such as leaf area index (LAI) can also be mapped to reveal spatial patterns in vegetation distribution and phenology. However, remote monitoring of carbon cycle process rates, such as net primary production (NPP) and net ecosystem production (NEP), remains challenging. Quantifying these flux rates is critical to understanding the role of the biosphere in regulating atmospheric carbon dioxide (CO₂) concentration.

Ecosystem process models are important tools for applying the information provided by remote sensing products to quantify fluxes of carbon and other elements. Physiologically based process models, applied in a spatially distributed mode, can assimilate and effectively integrate a diverse assemblage of environmental data, including information on soils, climate, and vegetation. Many of the relevant data on vegetation are now available from remote sensing, and the integration of remote sensing and process modeling is a rapidly evolving field (Cohen and Goward 2004).

The emerging capabilities for monitoring carbon pools and fluxes at relatively high spatial and temporal resolution are finding numerous applications, notably with respect to meeting the requirements of the United Nations Framework Convention on Climate Change to produce carbon emission

inventories that include the effects of land use (e.g., Chen et al. 2003). At the regional scale, comparison of carbon cycle processes from years with different seasonal and annual weather patterns can give an indication of potential regional responses and biospheric feedbacks to climate change. Landscape- and regional-scale mapping of carbon fluxes is also needed to provide local validation of the global measures of NPP products from coarse-resolution sensors such as MODIS (Moderate Resolution Imaging Spectroradiometer; Running et al. 2004) and to evaluate the carbon flux estimates derived from inverse modeling (Ciais et al. 2000). In this article, we outline remote sensing capabilities in relation to carbon cycle modeling and present examples of studies in three North American regions to demonstrate specific applications of an integrated remote sensing and modeling approach.

David P. Turner (e-mail: david.turner@oregonstate.edu) is an associate professor of ecological modeling in the Department of Forest Science, Oregon State University, Corvallis OR 97331. Scott V. Ollinger is an assistant professor of forest ecosystem analysis and remote sensing at the Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824. John S. Kimball is an assistant professor of hydrology and ecology research at Flathead Lake Biological Station, Division of Biological Sciences, University of Montana, Missoula, MT 59812. © 2004 American Institute of Biological Sciences.

Models as platforms for data synthesis and integration

The rapidly proliferating volume of spatial data generated by remote sensing has created a significant challenge in terms of designing algorithms that optimally assimilate, integrate, and distill these data into useful information. A spatially distributed process model uses spatial data to define initial conditions (e.g., land-cover type) or as primary drivers for computing biophysical processes (e.g., daily temperature). A major benefit to using process models for scaling purposes is that they can estimate many measurable variables; the model algorithms thus represent hypotheses that can be assessed and potentially revised after confrontation with observations.

Depending on the scientific objectives or applications, carbon cycle models have been designed with varying degrees of aggregation with respect to ecosystem processes, components, and time steps. Models also vary widely in how much they use remotely sensed input. For the purposes of assessing impacts of future climate change, a model must be able to determine its own biogeography and biogeochemistry primarily on the basis of climate and edaphic conditions. However, if the objective is simply monitoring current NPP, a wide variety of remotely sensed data could potentially be used.

Because the relatively simple models based on light-use efficiency (see Running et al. 2004) focus on current vegetation condition and do not include ecological and biogeochemical processes, they are generally not suitable for capturing changes in carbon flux over the course of forest succession. Since these changes can be a major factor in characterizing actual forest carbon flux for a specific area, more complex models may be needed for some applications. The most complex models, such as *ecosys* (Grant et al. 2003), are designed primarily to improve understanding of ecosystem function and to investigate potential impacts of environmental change at the site level. These models tend to have input requirements that are not feasibly generated in a spatial mode. Here we focus on ecosystem process models of intermediate complexity, such as PnET-CN and Biome-BGC (table 1). These models were designed to capture important ecosystem processes using generalized response functions that can be applied across large areas.

Remote sensing of vegetation properties in relation to modeling

Prescribing initial conditions for a spatially distributed model run affords important constraints on model behavior. These initial conditions may include both categorical and continuous variables.

Land cover. Specifying the type of land cover is an important first step in the implementation of a spatially distributed carbon cycle model, because vegetation cover types differ widely in their allometry and physiology. These differences in morphological and ecophysiological attributes are the result of adaptations to specific environments (Reich et al. 1997).

Broadleaf deciduous forests, for example, have very different structural and environmental response characteristics than grassland or evergreen coniferous forests, even though these vegetation types often occupy the same physiographic regions. Whereas differences in plant functional attributes can be observed and quantified at the plot scale, land-cover maps based on remote sensing provide the means to extrapolate local observations across large regions. Although spatial variation in the attributes of vegetation within a cover type can also be important, the relative consistency of these functional adaptations within cover types has proved to be enormously useful to modelers when combined with spatial data for land-cover characteristics. In this way, vegetation parameters required by models (e.g., leaf mass per unit area and maximum stomatal conductance) can be estimated spatially and allowed to interact with information on climate, soils, or other environmental factors (Ollinger et al. 1998).

In an effort to standardize land-cover classification at the global scale, the International Geosphere-Biosphere Programme has developed a 15-class scheme based on general structural characteristics of global vegetation and other land-cover features. This degree of disaggregation roughly matches the capability of sensors such as the Landsat Thematic Mapper to isolate different classes of land cover. An alternative to vegetation classification is provided by the “continuous fields” for life form, leaf type, and leaf longevity that are being developed from 500-meter (m) MODIS data. These surfaces make maximum use of multitemporal satellite data and will be increasingly useful for model initialization in regional applications.

Forest stand age class. Change in NPP with stand age is a well-recognized phenomenon, even though the mechanisms underlying this change remain controversial (Gower et al. 1996). Temporal patterns in NEP over relatively long-term successional stages within a cover type are also generally understood because of the strong carbon source associated with woody residues in early succession and the accumulation of stem wood and woody debris in mid to late succession (Janisch and Harmon 2002). If stand age is specified by remote sensing, carbon cycle process models can be run over the course of succession, improving their ability to accurately simulate NPP and NEP (Thornton et al. 2002, Law et al. forthcoming).

Classification based on remote sensing is the most common approach to assessing regional patterns of forest stand age, because it requires only one image and is relatively efficient compared to field inventory approaches. The changes in reflectance with stand age that permit classification are associated with differences in the proportion of ground surface that is exposed, in the spectral characteristics of the foliage (including epiphytic lichens), and in the structural properties of the canopy, which influence patterns of shading. In moist tropical forests, several stages of succession can be separated using the Landsat Enhanced Thematic Mapper Plus (ETM+) sensor by relying on differences in red and near-infrared reflectances (Moran et al. 1994). In the Pacific

Table 1. Comparison of ecosystem models at different levels of aggregation.

Model name	Time step	Features	Reference
TEM	Monthly	Rate parameters calibrated with observed net primary production	Raich et al. 1991
PnET-CN	Monthly	Maximum photosynthetic rate determined by foliar nitrogen concentration	Aber et al. 1997
Biome-BGC	Daily	Photosynthesis and transpiration based on stomatal conductance	Thornton et al. 2002
SPA	Hourly	Water balance (includes root and stem resistance and plant capacitance)	Williams et al. 2001

Northwest, reflectances in the midinfrared wavelengths have also been included in age-based classification schemes (Cohen et al. 1995). Classification accuracies on the order of 80% are generally achieved in these studies. An alternative, more precise approach to estimating stand age is the analysis of change detection using multiple images (Hall et al. 1991, Cohen et al. 2002). This approach is particularly desirable for modeling NEP in the first few years of succession, when heterotrophic respiration is high and NPP is low.

Leaf area index. Specifying LAI from remote sensing is particularly informative when models include canopy light extinction and other processes that vary with canopy depth. There is usually a significant correlation of LAI to spectral vegetation indexes such as the normalized difference vegetation index (NDVI) because of the variable red and near-infrared spectral reflectance properties of photosynthetic material. However, the relationship tends to be asymptotic, with saturation at LAI levels on the order of three to five (Turner et al. 1999). Forest LAI has also been estimated using airborne lidar (light detecting and ranging) sensors, and the relationship of field-measured LAI to lidar data is not asymptotic (Lefsky et al. 1999). Lidar, like the combination of hyperspectral data and interferometric synthetic aperture radar (InSAR), has the added capability of characterizing the distribution of foliage with height in the canopy (Lefsky et al. 2002, Treuhaft et al. 2002, 2004).

Besides the maximum seasonal LAI, some carbon cycle models also assimilate spatial information on seasonal changes in LAI (e.g., Liu et al. 1999) or dates for the beginning of leaf-out and the beginning and end of leaf drop. For Earth-orbiting sensors with daily coverage, it has been demonstrated that compositing over intervals of 8 days or more to avoid problems with cloudiness generally permits reliable monitoring of leaf phenology. Capturing the seasonal trajectory of LAI in ecosystems such as grasslands and deciduous forests is now possible at spatial resolutions as fine as 250 m with MODIS data (Zhang et al. 2003). Since interannual variation in NPP and NEP is significantly affected by the length of the growing season (Kimball et al. forthcoming), knowing the timing of green-up and leaf drop is of great value.

Foliar nitrogen. The positive relationship between leaf nitrogen and photosynthetic capacity has become one of the most enduring results of modern ecophysiology and is at the core

of a number of ecosystem models. The basis of this relationship is that most of the nitrogen in plant foliage is contained within proteins and carboxylating enzymes that are associated with photosynthesis (e.g., rubisco [ribulose biphosphate carboxylase/oxygenase]).

Evidence supporting the role of canopy nitrogen concentrations as a scalar for carbon uptake comes from both theoretical and empirical studies. Because nitrogen is often the limiting nutrient in terrestrial ecosystems, it has been argued that natural selection should favor individuals that allocate nitrogen through the canopy in an efficient manner. This notion has also been borne out through field studies showing strong relationships among NPP, canopy-level nitrogen concentrations, and rates of nitrogen mineralization in soils (Reich et al 1997, Smith et al. 2002). Recently, Green and colleagues (2003) compiled data from a variety of C_3 plant communities and found that most of the variation in canopy light-use efficiency could be explained by variation in leaf nitrogen.

An obvious extension of these results is that methods for detecting canopy nitrogen concentrations can substantially improve the accuracy of spatially explicit model applications. Methods for detecting canopy nitrogen using airborne remote sensing at high spectral resolution have been available for some time (see Smith et al. 2002), and one of the authors of this article (S. V. O., working with Marie-Louise Smith) recently showed that this approach increased the prediction accuracy of a productivity model applied in the White Mountains region of New Hampshire. However, broader application of canopy nitrogen detection has thus far been limited by the availability of hyperspectral data and by the small spatial coverage of the instruments that are currently available. Given the critical importance of nitrogen as a rate-limiting factor in terrestrial carbon cycling, and the continued development of new hyperspectral sensors (e.g., the space-based Hyperion instrument, launched in November 2000), expanded application of this approach can be expected in the future (Ustin et al. 2004).

Biomass. Knowledge of the amount of vegetation biomass is a strong foundation for simulating local carbon budgets. The mass of living material is often used to initialize vegetation carbon pools for regional model simulations (Kimball et al. 2000) and is particularly important for estimating autotrophic respiration. Stem mass is also indicative of the detri-

tal residues that would support increased heterotrophic respiration after a disturbance.

Optical (i.e., visible and infrared) and microwave wavelengths have varying sensitivities to aboveground vegetation biomass. Optical remote sensing methods, such as empirical and statistical regression models with NDVI, have been used to estimate the amount and temporal variability in aboveground biomass (Dong et al. 2003). These techniques are largely sensitive to green leaves; methods for extracting information for other biomass components, such as stems and roots, generally require detailed ancillary information on vegetation allometry and the relative fraction of photosynthetic and nonphotosynthetic components of biomass. Optical remote sensing methods also show an asymptotic relationship to biomass and are increasingly insensitive to biomass levels above a threshold that varies from 50 to 80 megagrams (Mg) per hectare, depending on vegetation type and structure (Dong et al. 2003).

Synthetic aperture radar (SAR) and other remote sensing systems based on active microwaves are also sensitive to vegetation structure and to the amount of biomass, including both photosynthetic (green) and nonphotosynthetic vegetation components. Microwave wavelengths penetrate to greater depths in plant canopies than optical sensors do and generally show more promise for assessing standing woody biomass (Kasischke et al. 1997). Radar sensitivity to vegetation biomass is strongly dependent on wavelength, with longer wavelengths (L-band) generally able to detect greater vegetation volumes and biomass levels than shorter wavelengths (C-band). Like optical remote sensing, radar shows an asymptotic relationship to vegetation biomass, although saturation levels for longer microwave wavelengths are much higher than those for optical sensors. Single-band radar can detect aboveground biomass up to approximately 100 Mg per hectare; multiband and multipolarization radar can extend this range up to approximately 200 Mg per hectare (Dobson et al. 1992, Luckman et al. 1998). Multiband radar also enables separation of biomass into component fractions (e.g., stem and canopy) (Saatchi and Moghaddam 2000). Recent research with lidar and InSAR sensors has shown promise for increasing the maximum biomass that can be detected through remote sensing (Lefsky et al. 1999, Treuhaft et al. 2004).

Canopy height. One hypothesis for the decline in forest NPP with stand age is that hydraulic limitations associated with tree height, notably the path length of transpired water and the force of gravity, begin to constrain stomatal conductance (Hubbard et al. 1999). Canopy height and density are also important factors regulating wind velocity, surface roughness, canopy resistance to evapotranspiration, and carbon exchange. These mechanisms are beginning to be incorporated into ecosystem process models (Williams et al. 2001). Lidar sensors are very effective at determining canopy height (Lefsky et al. 2002). InSAR is less accurate, but it has the advantage of more readily covering large areas (Treuhaft et al. 2004). Thus, as extensive mapping of tree height becomes

possible, the information will be readily used as input for models. Canopy height, as a function of stand age, is also a traditional indicator of site quality, so the combination of stand height from remote sensing and stand age from change-detection analysis (also based on remote sensing) could be used in validation of modeled bolewood (i.e., stem) production.

Combining models with remote sensing: Representative applications

Recent scaling studies have combined remote sensing with ecosystem process models to evaluate components of the carbon cycle in three different regions of North America (the northeastern United States, the Canadian boreal forest, and the Pacific Northwest). A common feature of these studies is the strong interdisciplinary nature of their research.

Northeastern studies. The northeastern United States is of interest to scientists studying the carbon cycle, both because it is currently an important carbon sink (Turner et al. 1995) and because it has been heavily influenced by a variety of physical and chemical stress factors, including historical human land use and elevated inputs of several atmospheric pollutants. Carbon cycling in the Northeast (specifically New York and New England) has been evaluated on a regional scale in a variety of contexts. These efforts have required researchers to develop spatial coverages (geographic data layers, or polygon maps used for studying geographic relationships) that included the data on climate, land cover, and vegetation needed to drive carbon flux models.

In a series of studies using the PnET forest ecosystem model (e.g., Aber et al. 1995, Ollinger et al. 1998), land-cover data at 1-kilometer (km) resolution were generated from AVHRR (Advanced Very High Resolution Radiometer) imagery. Coverages for climate, radiation, and atmospheric nitrogen deposition variables were derived using available station data, coupled with a 1-km digital terrain model. Examination of the patterns in predicted NPP and climate input variables revealed a difference in the apparent controlling factors for NPP in deciduous and evergreen forests. Within areas classified as deciduous forest, patterns of predicted NPP were strongly correlated with annual precipitation, suggesting that water was an important limitation on regional growth. Predicted NPP for areas classified as evergreen, however, was more strongly related to temperature and to the length of the growing season, suggesting a greater role for energy limitation and a lesser role for moisture stress (figure 1).

A limitation of this analysis was that data inputs for certain vegetation parameters, most notably the concentration of nitrogen in foliage, were not available in a spatially explicit format and had to be held constant within each vegetation type that occurred in the land-cover classification (deciduous, pine, or spruce-fir forest). Although this limitation applies to most modeling studies, the ability to specify explicit foliar nitrogen values is especially important for eastern deciduous forests, where variation in growth is strongly related to nitrogen concentrations but poorly related to LAI (Smith et al. 2002).

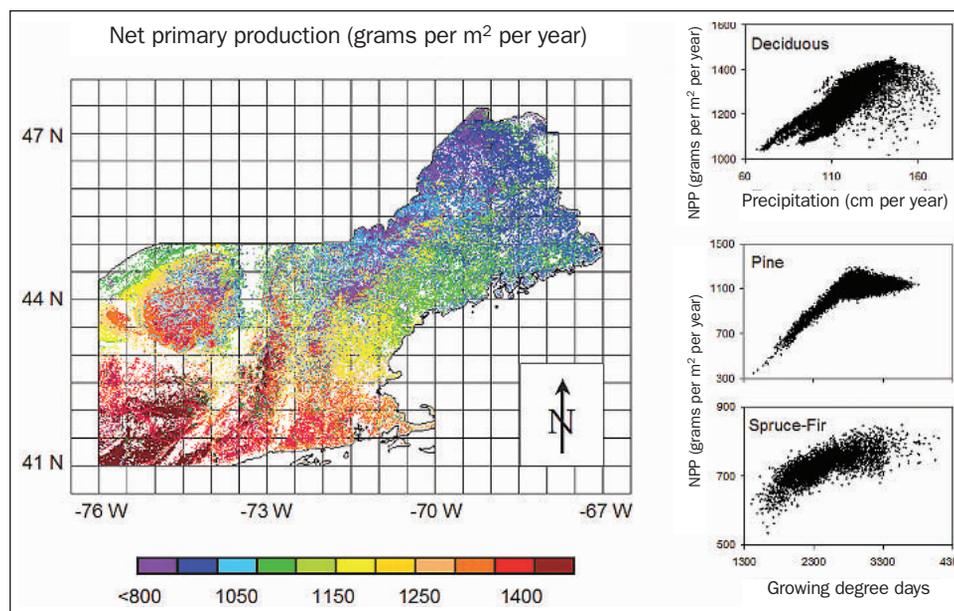


Figure 1. Net primary production, or NPP, in grams of carbon per square meter per year (1-kilometer resolution), simulated by the PnET model for the northeastern United States using land-cover data from remote sensing (left). Simulated NPP for three cover types (right) is strongly related to annual precipitation (for deciduous forests) or to annual growing degree days (for pine and spruce-fir forests).

Given the absence of data layers for canopy nitrogen at the regional scale, a subsequent investigation was carried out (by S. V. O. and Marie-Louise Smith) over a smaller landscape surrounding the Bartlett Experimental Forest (BEF) in northern New Hampshire. A spatial coverage for canopy nitrogen was derived using remotely sensed data at high spectral resolution from the aircraft-based Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) sensor operated by the National Aeronautics and Space Administration (NASA). In this study, the PnET model was run at 18-m spatial resolution using AVIRIS-derived canopy nitrogen inputs. As a means of testing the benefit of canopy nitrogen detection, an additional set of runs was conducted using mean foliar nitrogen values for deciduous and evergreen stands, mimicking the approach used when data at high spectral resolution are not available. Comparison of simulated wood growth against field measurements at 38 field validation plots (figure 2) produced a predicted r^2 of 0.74, which was a substantial improvement over predictions generated using mean foliar nitrogen ($r^2 = 0.37$).

An interesting outcome of this work was that, at the scale represented by the BEF (approximately 5 by 5 km), the factor that explained most of the variation in predicted and observed productivity was foliar nitrogen (figure 2), with much smaller degrees of variation caused by climatic variables. This apparent contrast with results observed for the Greater Northeast reflects the different degrees of variation these factors exhibit over different spatial scales. At BEF, local variation in foliar nitrogen is substantial; the range of nitrogen measurements for the forest is almost as great as the range for the entire region. In contrast, temperature and precipitation

typically vary more widely at regional and continental scales than within local landscapes. Although local variation in climate can be important, particularly in areas of complex topography, the range of temperature and precipitation experienced at BEF is small compared with the broad gradients that occur over larger geographical regions.

Boreal Ecosystem-Atmosphere Study. The Boreal Ecosystem-Atmosphere Study (BOREAS) was an international, multi-disciplinary effort to improve understanding of the structure and function of the boreal forest biome (Sellers et al. 1997). Recent evidence of increased warming in Canada's boreal forests—a trend that has been linked to global climate change—has generated great interest from the scientific community, particularly in light of the potential for large positive feedbacks to regional and global weather and carbon cycles. Thus, researchers have endeavored to clarify the interactions of boreal forest processes with climate and to examine the role of these forests in the terrestrial carbon cycle. A major focus of BOREAS was the development and evaluation of an integrated surface measurement network, along with approaches based on ecological models and remote sensing, for the temporal and spatial extrapolation of forest biomass, productivity, and net carbon exchange.

A primary requirement of the regional ecological modeling efforts in BOREAS was relevant land-cover classification. Biophysical and meteorological measurements, including tower-based eddy covariance measurements, were made at a network of sites within the region. These measurements revealed marked differences in energy exchange and carbon

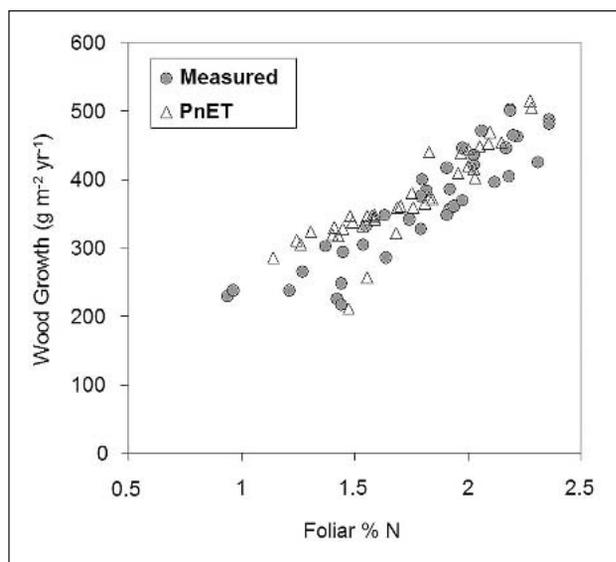


Figure 2. The relationship between foliar nitrogen (N) concentration (as a percentage of leaf mass) and wood growth (in grams of carbon per square meter per year) for 38 growth-inventory plots at the Bartlett Experimental Forest in north-central New Hampshire. Shaded symbols show the field-measured relationship; open symbols show the predicted relationship, generated by combining remotely sensed canopy nitrogen estimates (from the Airborne Visible/Infrared Imaging Spectrometer, or AVIRIS) with the PnET ecosystem model.

cycle dynamics among needleleaf coniferous and broadleaf deciduous forests, as well as major differences between forests and wetlands. Initially, many of these critical features were poorly delineated using optical remote sensing approaches that had been successfully used for other biomes at relatively coarse spatial resolution (i.e., > 1 km). Subsequent ecological modeling studies revealed that adequate representation of subgrid-scale land-cover heterogeneity, particularly between deciduous forests, coniferous forests, and wetlands, is critical for accurate regional extrapolations of boreal carbon exchange dynamics (e.g., Kimball et al. 1999).

BOREAS researchers made a major effort to develop improved remote sensing products for initializing and verifying model simulations of carbon exchange. A significant lesson learned during the study was that, at high latitudes, the application of satellite-based optical remote sensing methods for landscape assessment and monitoring was limited by frequent cloud cover, smoke, and other atmospheric aerosol effects, as well as low sun angles and reduced solar illumination for much of the year. Radar remote sensing, however, was found to be particularly useful for these environments because of its sensitivity to surface texture, biomass, and dielectric properties and its ability to operate by night or day, under virtually any weather conditions.

Of special interest was the finding that satellite information on daily radar backscatter from the K_u -band NASA Scatterometer, or NSCAT, was sensitive to the timing of primary spring thaw and fall freeze events, which corresponded with tower eddy covariance measurements and with ecological model simulations of seasonal shifts in net CO_2 exchange (Frolking et al. 1999). Results of ecological model simulations and of studies measuring tower eddy flux showed that annual NPP and NEP for boreal forests are particularly sensitive to the timing of spring thaw and to the duration of the growing season (Kimball et al. 2000). Subsequent analyses of records from long-term, satellite-based active and passive microwave remote sensing, and of long-term simulations of stand carbon exchange, revealed strong linkages between the timing of the primary spring thaw event and the annual net carbon exchange for boreal coniferous and deciduous stands (see figure 3). Airborne and satellite remote sensing based on SAR was also employed to improve land-cover mapping, particularly for wetlands, and to quantify spatial and temporal patterns in vegetation (crown and stem) biomass (Saatchi and Mughaddam 2000).

As in the northeastern studies, a major factor that BOREAS did not directly address was the role of disturbance (e.g., fire, land management, insects) in shaping the boreal landscape and determining the carbon cycle dynamics of the boreal forest. Initial land-cover classifications for the region, derived from NDVI data at 1-km resolution gathered using AVHRR, indicated that approximately 30% of the region was directly affected by fire disturbance during the 30- to 35-year period before 1992 (Steyaert et al. 1997). Disturbances from insect defoliation, logging, and agriculture-related deforestation are also known to play an important role in shaping land cover, the age distribution of forest stands, and associated carbon budgets for the region. BOREAS follow-on investigations have attempted to address some of these deficiencies.

Pacific Northwest study. The Pacific Northwest, with its old-growth temperate rain forests, has some of the highest carbon densities on the planet. The rates of NPP and NEP are also relatively high, depending on stand age and location (Law et al. forthcoming), and the region has been subject to intensive logging over the last 100 years (Garman et al. 1999). Thus, like the Northeast, the Pacific Northwest is of great interest to researchers trying to understand the carbon cycle.

Forest carbon budgets for the Pacific Northwest have been constructed on landscape to regional scales, using forest inventory data (Turner et al. 1995) and remote sensing of land cover and disturbance (Cohen et al. 1996). More recent efforts have included remote sensing of LAI and implementation of change detection for aging of forest stands (Turner et al. 2003a). The process model used in the recent Pacific Northwest studies is Biome-BGC (Thornton et al. 2002), which estimates heterotrophic respiration as well as NPP. To account for heterotrophic respiration, particularly as it is influenced by stand age, the model must be “spun up” (i.e., run over 1000

years or more) to bring the slow-turnover soil carbon pools into near equilibrium with the local climate. At the end of the spin-up, a disturbance such as clear-cut logging is simulated, and the model is run forward to an age specified by the remote sensing analysis. Site water balance (in part a function of soil depth) strongly regulates LAI in the Pacific Northwest; thus, the spin-ups are run at a range of soil depths for each grid cell, to determine a depth that results in agreement between modeled and remotely sensed LAI.

At the landscape scale, the implementation of this combination of remote sensing and modeling (figure 4) revealed the strong influence of stand age-class distribution on areawide NEP (Turner et al. 2003a). Without including the age-class specification, the simulated landscape-scale NEP was 50 grams (g) carbon per square meter per year in the central Cascade Mountains in Oregon (a small carbon sink), compared with more than 200 g carbon per square meter per year for the same area with the stand age class specified by the ETM+ sensor. In an application over a much larger domain, the dominant control on NPP and NEP was the water balance gradient that extends inland from the Pacific coast (Law et al. forthcoming). For all locations, the simulations showed a strong interannual variation in NPP, associated primarily with the degree of summer drought.

Validation of model-based carbon flux estimates in the Pacific Northwest has been approached at multiple scales (Law et al. forthcoming). Comparing the daily gross primary production (GPP) and NEP as simulated by the model with the same measures as estimated from eddy covariance data made it possible to assess model sensitivity to daily weather. To evaluate model behavior over a successional sequence, field measurements of NPP and NEP at a chronosequence of plots in different climatic zones were compared with model simulations of NPP and NEP at the stand locations. At the regional scale, data from the permanent plot network of the USDA (US Department of Agriculture) Forest Service's Forest Inventory and Analysis program provided a spatially extensive data set for validation of the Biome-BGC model. However, the inventory data have considerable limitations in terms of converting the raw measurements of tree diameters to estimates of carbon pools and flux (Jenkins et al. 2001). Because the exact locations of the inventory plots are not released, comparisons of measured (figure 5) and simulated stem production were made within age-class bins at the ecozone scale to examine overall bias and age trends in production.

Selected research challenges

The increasing availability of spatial data and the growing interest in quantifying terrestrial carbon flux have driven

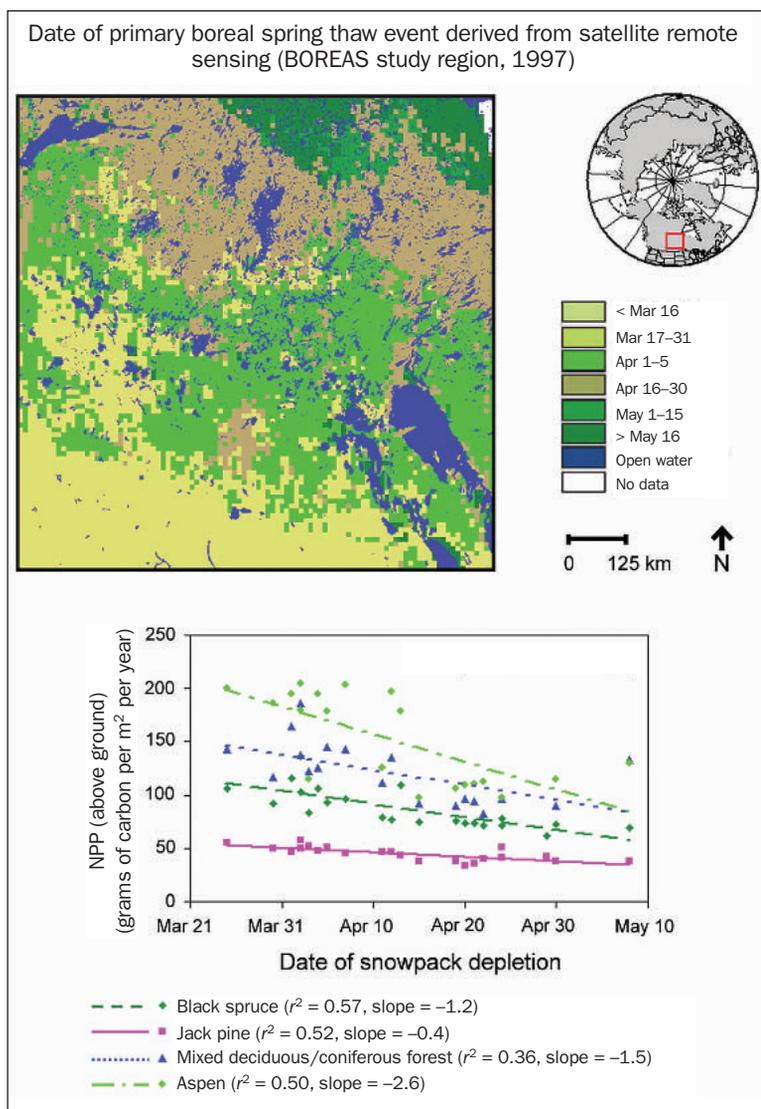


Figure 3. Satellite remote sensing (top) of the 1997 primary spring thaw event for the Boreal Ecosystem–Atmosphere Study (BOREAS) study region, derived from temporal classification of daily radar backscatter information from the NASA (National Aeronautics and Space Administration) Scatterometer, or NSCAT. The dates in the legend represent the interval during which thaw occurred. Graph (bottom panel) shows the relationship between measurements of aboveground net primary production (NPP) for different forest types by year within the study region and corresponding estimates of snowpack depletion, a surrogate measure of spring thaw timing. Years with an early spring tend to promote greater annual NPP, whereas years with a delayed spring promote the opposite response. Adapted from Kimball and colleagues (2000, forthcoming).

rapid progress in the integration of modeling and remote sensing. Some of the key challenges at this point relate to algorithm development and the interpretation or validation of resulting products.

Resolving aggregation issues. There is an unavoidable tension in carbon flux scaling studies between spatial resolution

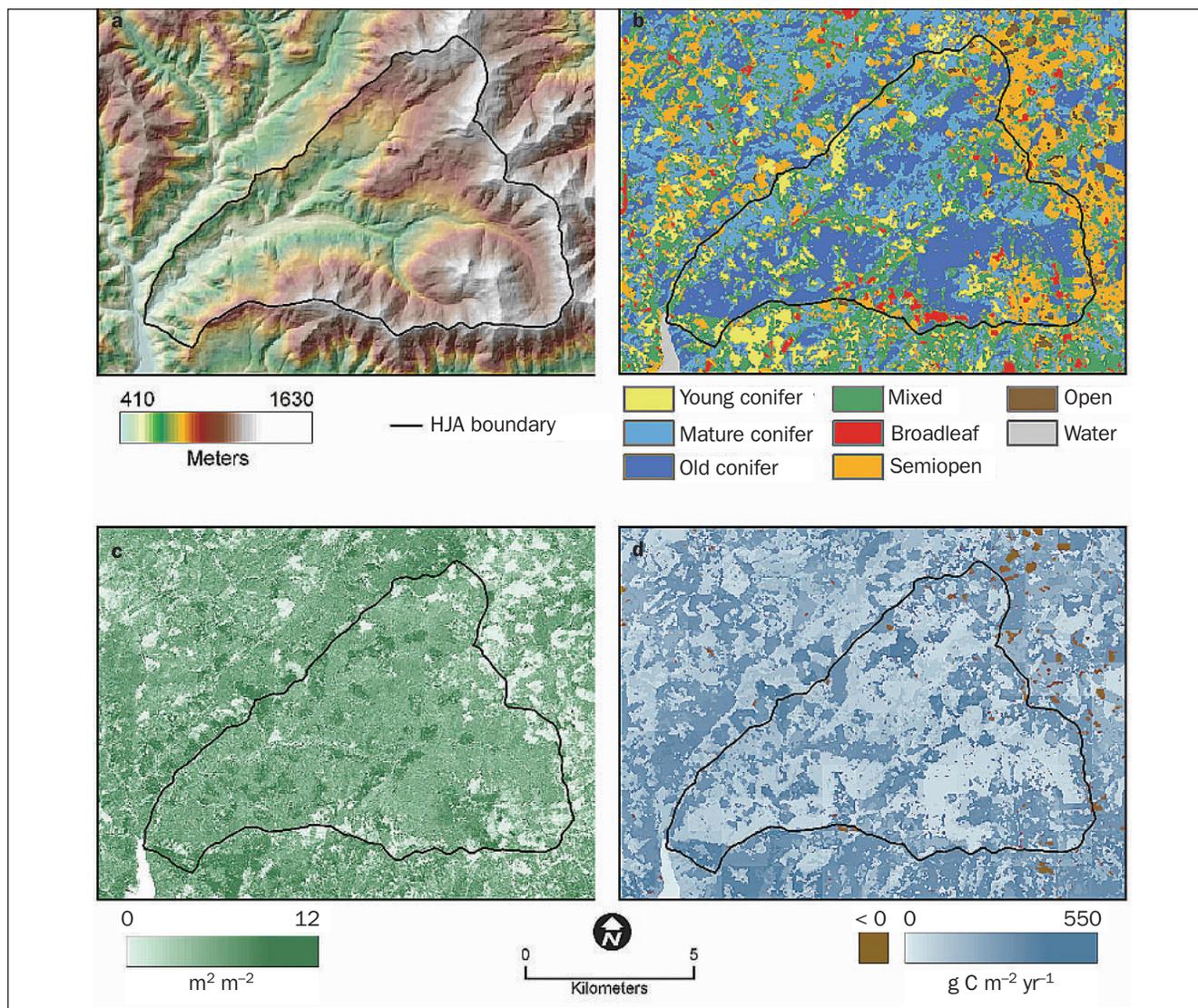


Figure 4. Landscape-scale application of the Biome-BGC model with inputs of land cover and leaf area index from remote sensing: (a) shaded relief, (b) land cover, (c) leaf area index (in square meters of leaf area per square meter of ground), and (d) net ecosystem production (in grams of carbon per square meter per year). “HJA” refers to the H. J. Andrews Experimental Forest. Adapted from Turner and colleagues (2003a).

and spatial extent. Process models tend to be computationally demanding, especially if a long spin-up is required. Thus, it may not be feasible to scale NPP and NEP over millions of square kilometers at the 30-m resolution of the ETM+ sensor. Comparisons of pattern and process at coarse and fine scales over the same domain often reveal scale dependence in model inputs and outputs (Moody and Woodcock 1995, Kimball et al. 1999). New strategies are needed to diagnose and, if need be, compensate for this scale dependence.

Screening algorithms that detect the scale of spatial heterogeneity in land cover based on high spatial resolution spectral reflectance could potentially be used to differentiate between relatively homogeneous areas and the heterogeneous areas where a fine spatial resolution (< 1 km) may be needed. Analysis of spatial autocorrelation with Landsat Thematic

Mapper imagery in the Pacific Northwest suggests that at resolutions coarser than 250 m, the pattern of dispersed clear-cuts begins to be lost (Turner et al. 2000).

The potential problems with temporal resolution are analogous to those with spatial resolution in many respects. Leaf-level measurements with cuvettes, and ecosystem-level measurements with eddy covariance flux towers, reveal that basic physiological processes such as photosynthesis and plant respiration respond quite rapidly (and often in a non-linear fashion) to environmental drivers such as temperature and irradiance. However, running a half-hourly time-step model over a large area for multiple years is often not feasible, not only for computational reasons but also because of the difficulty of providing meteorological data for each grid cell at each time step. One alternative approach has been to

develop process models using data at fine temporal resolution for model calibration (e.g., half-hourly eddy covariance flux data) and to run the models for a wide range of environmental conditions, subsequently aggregating results to a coarser time step to create response surfaces or parameterizations for much simpler model forms (Williams et al. 1997). The simpler model is then used in scaling applications.

Distinguishing the effects of canopy structure and chemistry in carbon flux studies. In forested ecosystems, the canopy properties that have been examined as potential scalars between remotely sensed imagery and carbon flux simulation models can be generalized into two groups: (1) structural properties, such as canopy biomass and LAI, and (2) biochemical variables, such as chlorophyll and nitrogen concentrations. Although there is a reasonably firm understanding of the roles played by each of these variables at specific sites, the degree to which broadscale patterns of terrestrial carbon uptake reflect variation in canopy structure rather than chemistry is not well understood.

Remote sensing is quite effective in quantifying LAI at relatively low levels. When LAI is low, the relationship of LAI to NPP is strong, because a higher LAI means more absorbed photosynthetically active radiation (APAR). However, when LAI is higher (> 4), the fraction of incident photosynthetically active radiation that is absorbed by the canopy is often close to 1, and therefore APAR does not increase appreciably with increasing LAI. At that point, additional structural, compositional, and biochemical factors gain importance as determinants of productivity. These include the following:

- The distribution of LAI among different heights in the canopy (detectable by lidar and InSAR), which affects the ratio of direct to diffuse light in the canopy and hence the efficiency of light use.
- The variation among species in shade tolerance and in corresponding light-use efficiency.
- The variation in foliar nitrogen concentration among sites, and among species within a site, which strongly influences productivity (Smith et al. 2002).

It is also evident that decreases in foliar nitrogen concentration late in the growing season are correlated with decreases in canopy light-use efficiency that are independent of changes in LAI (Wilson et al. 2001, Turner et al. 2003b).

Although regional- and continental-scale variation in foliar nitrogen has been observed empirically and predicted by optimal nitrogen allocation models (e.g., Haxeltine and Prentice 1996), detecting nitrogen concentrations at broad spatial scales has not been accomplished. The successful launch of the Hyperion sensor, which operates at high spectral resolution (220 channels) and at 30-m spatial resolution (an effective resolution for vegetation surveys), provides opportunities for research at a growing number of sites (Ustin et al. 2004). The technical challenges that must be met to make optimal use of these data include dealing with

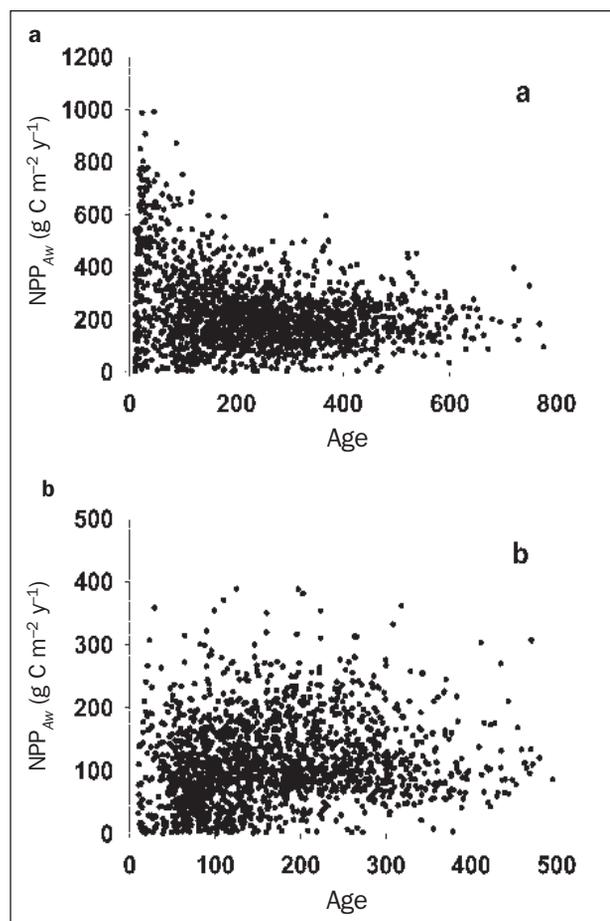


Figure 5. Aboveground wood net primary production (NPP_{Aw} ; grams of carbon per square meter per year) and stand age (years) at permanent plots managed by the USDA (US Department of Agriculture) Forest Service's Forest Inventory and Analysis Program in two ecozones, (a) the western Cascades and (b) the eastern Cascades. Adapted from Law and colleagues (forthcoming).

large volumes of data, improving methods for atmospheric correction, and developing broadly applicable relationships between spectral data and measured biochemical constituents.

Validating estimates of carbon flux at coarse spatial resolutions. The successful deployment of the MODIS sensor now permits estimation of GPP every 8 days, and of NPP on an annual basis, for every square kilometer of Earth's terrestrial surface (Running et al. 2004). A critical scaling issue related to the task of validating products from coarse-resolution sensors such as MODIS involves matching the scale of ground measurements to the scale of the sensor products. NPP is typically measured in plots or subplots ranging from 1 to 100 m² (Gower et al. 1999); thus, it is not feasible to measure NPP from wall to wall in a coarse-resolution grid cell. For NPP, the best alternative may be to use remote sensing and modeling at fine spatial resolution (10 to 30 m), in which the

size of the grid cells more nearly matches the size of the validation plots. For GPP and NEP, validation measurements can be derived from NEP measurements at the scale of a flux tower footprint (usually < 1 km²). For these measurements, as for NPP, validation can be accomplished by first using fine-scale remote sensing and modeling rather than direct comparison to MODIS GPP, which tends to be compromised by uncertainty about footprint location and by data gaps in the tower data. The high-quality meteorological observations at the tower can be used as model drivers, and GPP estimates from tower data can be used for validation of modeled GPP (Turner et al. 2003c).

The regional scaling of NPP or NEP based on remote sensing and process models will also eventually provide validation of land surface flux estimates derived from inverse modeling (e.g., Ciais et al. 2000). The inversion approach currently relies on flask samples, which significantly constrains the spatial resolution of the output (i.e., continental scale). However, new satellite-borne sensors under development will have the capability to measure total column and vertical profile abundance of CO₂ and thus to monitor spatial and temporal patterns in CO₂ concentration much more comprehensively (Engelen et al. 2001). The associated carbon flux estimates derived from inverse modeling, therefore, will have higher spatial and temporal resolution and will be amenable to validation with regional flux estimates generated from satellite data and process models.

Meeting the commitments of the United Nations Framework Convention on Climate Change.

The UN framework convention, adopted internationally in 1994, calls for participating countries to deliver periodic inventories of greenhouse gas emissions, including the sources and sinks of CO₂ associated with land use. The simplest approach to estimating carbon flux is a change-in-stocks approach that relies on comprehensive inventories of vegetation biomass. Differences in total carbon storage at two points in time are divided by the relevant interval to obtain an annual flux estimate averaged over the interval. In forested regions at mid latitudes, this approach usually amounts to repeated surveys of a network of permanent plots maintained by federal agencies for the purposes of natural resource inventories (Birdsey et al. 1993). There are limitations to the inventory approach, in that relatively long intervals are required to resurvey all plots, sampling intensity may be low, and the results tend to reveal only a net effect (i.e., relatively little about the mechanisms accounting for the changes).

An integrated remote sensing and modeling approach can also produce an estimate of annual changes in carbon stocks. Such an approach has the benefit of being spatially and temporally explicit and of quantifying the full suite of carbon pools and fluxes, including changes associated with harvesting (Chen et al. 2003, Turner et al. 2004). The change-in-stocks and remote sensing and modeling approaches to estimating fluxes at a national level require quite different research infrastructures, but they are ultimately complementary. Both are

likely to play a role in the emerging US Carbon Cycle Science Program (within the US Global Change Research Program), whose primary objectives include producing carbon flux estimates relevant to the evolution of policy regarding global climate change.

Conclusions

Ecosystem process models have become important tools for scaling NPP and NEP over landscape to regional domains. Their power is largely derived from their ability to distill a wide array of diverse data into useful information and to force consistency among numerous discrete observational data sets. Satellite remote sensing is providing an increasing variety of spatial data layers that are potentially usable as model input or for validation of model output. The integration of process models and remote sensing is particularly effective for monitoring at landscape to regional scales, because at fine spatial and temporal resolutions it can resolve the major near-term controls on carbon fluxes, including land use, foliar biophysical characteristics, topography, and climatic gradients. Research challenges in this field include optimizing spatial and temporal resolution for specific applications, differentiating the relative influences of structural and chemical variables on ecosystem carbon fluxes, and systematically validating model-based flux estimates.

Acknowledgments

Support for this work was provided by the National Aeronautics and Space Administration (NASA) Terrestrial Ecology Program, the NASA Carbon Cycle Science Program (grant no. CARBON-0000-1234), the National Institute for Global Environmental Change (grant no. UNH901214-02), and the US Environmental Protection Agency's STAR (Science to Achieve Results) program (grant no. R-82830901-0).

References cited

- Aber JD, Ollinger SV, Federer CA, Reich PB, Goulden ML, Kicklighter DW, Melillo JM, Lathrop RG Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5: 207–222.
- Aber JD, Ollinger SV, Driscoll CT. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* 101: 61–78.
- Birdsey RA, Plantinga AJ, Heath LS. 1993. Past and prospective changes in U.S. forest ecosystems. *Forest Ecology and Management* 58: 33–40.
- Chen JM, Weimin J, Cihlar J, Price D, Liu J, Chen W, Pan J, Black A, Barr A. 2003. Spatial distribution of carbon sources and sinks in Canada's forests. *Tellus* 55B: 622–641.
- Ciais P, Peylin P, Bosquet P. 2000. Regional biospheric carbon fluxes as inferred from atmospheric CO₂ measurements. *Ecological Applications* 10: 1574–1589.
- Cohen WB, Goward SN. 2004. Landsat's role in ecological applications of remote sensing. *BioScience* 54: 535–545.
- Cohen WB, Spies TA, Fiorella M. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. *International Journal of Remote Sensing* 16: 72–746.
- Cohen WB, Harmon ME, Wallin DO, Fiorella M. 1996. Two decades of carbon flux from forests of the Pacific Northwest. *BioScience* 46: 836–844.
- Cohen WB, Spies TA, Alig RJ, Oetter DR, Maierperger TK, Fiorella M. 2002. Characterizing 23 years (1972–1995) of stand replacement

- disturbance in western Oregon forests with Landsat imagery. *Ecosystems* 5: 122–137.
- Dobson MC, Ulaby FT, LeToan T, Beaudoin A, Kasichke ES, Christensen N. 1992. Dependence of radar backscatter on coniferous forest biomass. *IEEE Transactions on Geoscience and Remote Sensing* 30: 412–415.
- Dong J, Kaufmann RK, Myneni RB, Tucker CJ, Kauppi PE, Liski J, Buermann W, Alexeyev V, Hughes MK. 2003. Remote sensing estimates of boreal and temperate forest woody biomass: Carbon pools, sources, and sinks. *Remote Sensing of Environment* 84: 393–410.
- Engelen RJ, Denning AS, Gurney KR, Stephens GL. 2001. Global observations of the carbon budget, pt. 1: Expected satellite capabilities for emission spectroscopy in the EOS and NPOESS eras. *Journal of Geophysical Research* 106: 20055–20068.
- Frolking S, McDonald K, Kimball J, Zimmermann R, Way JB, Running SW. 1999. Using the space-borne NASA Scatterometer (NSCAT) to determine the frozen and thawed seasons of a boreal landscape. *Journal of Geophysical Research* 104: 27895–27907.
- Garman SL, Swanson FJ, Spies TA. 1999. Past, present, and future landscape patterns in the Douglas-fir region of the Pacific Northwest. Pages 61–86 in Rochelle JA, Lehmann LA, Wisniewski J, eds. *Forest Fragmentation: Wildlife and Management Implications*. Boston: Brill.
- Gower ST, McMurtrie RE, Murty D. 1996. Aboveground net primary production decline with stand age: Potential causes. *Trends in Ecology and Evolution* 11: 378–382.
- Gower ST, Kucharik CJ, Norman JM. 1999. Direct and indirect estimation of leaf area index, f_{APAR} , and net primary production of terrestrial ecosystems. *Remote Sensing of Environment* 70: 29–51.
- Grant RF, Oechel WC, Ping C. 2003. Modelling carbon balances of coastal arctic tundra under changing climate. *Global Change Biology* 9: 16–36.
- Green DS, Erickson JE, Kruger EL. 2003. Foliar morphology and canopy nitrogen as predictors of light-use efficiency in terrestrial vegetation. *Agricultural and Forest Meteorology* 115: 163–171.
- Hall FG, Botkin DB, Strebel DE, Woods KD, Goetz SJ. 1991. Large-scale patterns of forest succession as determined by remote sensing. *Ecology* 72: 628–640.
- Haxeltine A, Prentice IC. 1996. A general model for the light-use efficiency of primary production. *Functional Ecology* 10: 551–561.
- Hubbard RM, Bond BJ, Ryan MG. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology* 19: 165–172.
- Janisch JE, Harmon ME. 2002. Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity. *Tree Physiology* 22: 77–89.
- Jenkins JC, Birdsey RA, Pan Y. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. *Ecological Applications* 11: 1174–1193.
- Kasichke ES, Melack JM, Dobson MC. 1997. The use of imaging radars for ecological applications—a review. *Remote Sensing of Environment* 59: 141–156.
- Kimball JS, Running SW, Saatchi SS. 1999. Sensitivity of boreal forest regional water flux and net primary production simulations to sub-grid scale land-cover complexity. *Journal of Geophysical Research* 104: 27789–27801.
- Kimball JS, Keyser AR, Running SW, Saatchi SS. 2000. Regional assessment of boreal forest productivity using an ecological process model and remote sensing parameter maps. *Tree Physiology* 20: 761–775.
- Kimball JS, McDonald KC, Frolking S, Running SW. Radar remote sensing of the spring thaw transition across a boreal landscape. *Remote Sensing of Environment*. Forthcoming.
- Law BE, Turner DP, Lefsky M, Campbell J, Guzy M, Sun O, Van Tuyl S, Cohen WB. Carbon fluxes across regions: Observational constraints at multiple scales. In Wu J, Jones B, Li H, Loucks O, eds. *Scaling and Uncertainty Analysis in Ecology*. New York: Columbia University Press. Forthcoming.
- Lefsky MA, Cohen WB. 2003. Selection of remotely sensed data. Pages 13–46 in Wulder MA, Franklin SE, eds. *Remote Sensing of Forest Environments: Concepts and Case Studies*. Boston: Kluwer Academic.
- Lefsky MA, Cohen WB, Acker SA, Parker GG, Spies TA, Harding D. 1999. Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir western hemlock forests. *Remote Sensing of Environment* 70: 339–361.
- Lefsky MA, Cohen WB, Parker GG, Harding DJ. 2002. Lidar remote sensing for ecosystem studies. *BioScience* 52: 19–30.
- Liu J, Chen JM, Cihlar J, Chen W. 1999. Net primary productivity distribution in the BOREAS region from a process model using satellite and surface data. *Journal of Geophysical Research* 104: 27735–27754.
- Luckman A, Baker J, Honzak M, Lucas R. 1998. Tropical forest biomass density estimation using JERS-1 SAR: Seasonal variation, confidence limits and application to image mosaics. *Remote Sensing of Environment* 63: 126–139.
- Moody A, Woodcock CE. 1995. The influence of scale and the spatial characteristics of landscapes on land-cover mapping using remote sensing. *Landscape Ecology* 10: 363–379.
- Moran EF, Brondizio E, Mausell P, Wu Y. 1994. Integrating Amazonian vegetation, land-use, and satellite data. *BioScience* 44: 329–338.
- Ollinger SV, Aber JD, Federer CA. 1998. Estimating regional forest productivity and water balances using an ecosystem model linked to a GIS. *Landscape Ecology* 13: 323–34.
- Raich JW, Rastetter EB, Mellilo JM, Kicklighter PA, Steudler PA, Peterson BJ, Grace AL, Moore BI, Vorosmarty CJ. 1991. Potential net primary productivity in South America: Application of a global model. *Ecological Applications* 1: 399–429.
- Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences* 94: 13730–13734.
- Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H. 2004. A continuous satellite-derived measure of global terrestrial primary production. *BioScience* 54: 547–560.
- Saatchi SS, Mughaddam M. 2000. Estimation of crown and stem water content and biomass of boreal forests using polarimetric SAR imagery. *IEEE Transactions on Geoscience and Remote Sensing* 38: 697–709.
- Sellers PJ, et al. 1997. BOREAS in 1997: Experiment overview, scientific results, and future directions. *Journal of Geophysical Research* 102: 28731–28769.
- Smith ML, Ollinger SV, Martin ME, Aber JD, Hallett RA, Goodale CL. 2002. Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. *Ecological Applications* 12: 1286–1302.
- Steyaert LT, Hall FG, Loveland TR. 1997. Land cover mapping, fire regeneration, and scaling studies in the Canadian boreal forest with 1 km AVHRR and Landsat TM data. *Journal of Geophysical Research* 102: 29581–29598.
- Thornton PE, et al. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needle-leaf forests. *Agricultural and Forest Meteorology* 113: 185–222.
- Treuhaft RN, Asner GP, Law BE, Van Tuyl S. 2002. Forest leaf area density profiles from the quantitative fusion of radar and hyperspectral data. *Journal of Geophysical Research* 107: 4568–4580.
- Treuhaft RN, Law BE, Asner GP. 2004. Forest attributes from radar interferometric structure and its fusion with optical remote sensing. *BioScience* 54: 561–571.
- Turner DP, Koerper GJ, Harmon ME, Lee JJ. 1995. A carbon budget for forests of the conterminous United States. *Ecological Applications* 5: 421–436.
- Turner DP, Cohen WB, Kennedy RE, Fassnacht KS, Briggs JM. 1999. Relationships between leaf area index and TM spectral vegetation indices across three temperate zone sites. *Remote Sensing of Environment* 70: 52–68.
- Turner DP, Cohen WB, Kennedy RE. 2000. Alternative spatial resolutions and estimation of carbon flux over a managed forest landscape in western Oregon. *Landscape Ecology* 15: 441–452.
- Turner DP, Guzy M, Lefsky MA, Van Tuyl S, Sun O, Daly C, Law BE. 2003a. Effects of land use and fine-scale environmental heterogeneity on net ecosystem production over a temperate coniferous forest landscape. *Tellus* 55B: 657–668.

- Turner DP, Urbanski S, Bremer D, Wofsy SC, Meyers T, Gower ST, Gregory M. 2003b. A cross-biome comparison of light use efficiency for gross primary production. *Global Change Biology* 9: 383–395.
- Turner DP, Ritts WD, Cohen WB, Gower ST, Zhao M, Running SW, Wofsy SC, Urbanski S, Dunn A, Munger JW. 2003c. Scaling gross primary production (GPP) over boreal and deciduous forest landscapes in support of MODIS GPP product validation. *Remote Sensing of Environment* 88: 256–270.
- Turner DP, Guzy M, Lefsky M, Ritts W, VanTuyl S, Law BE. 2004. Monitoring forest carbon sequestration with remote sensing and carbon cycle modeling. *Environmental Management* 25: 1961–1979.
- Ustin SL, Roberts DA, Gamon JA, Asner GP, Green RO. 2004. Using imaging spectroscopy to study ecosystem processes and properties. *BioScience* 54: 523–534.
- Williams M, Rastetter EB, Fernandes DN, Goulden ML, Shaver GR, Johnson LC. 1997. Predicting gross primary productivity in terrestrial ecosystems. *Ecological Applications* 7: 882–894.
- Williams M, Bond BJ, Ryan MG. 2001. Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. *Plant, Cell and Environment* 24: 679–690.
- Wilson KB, Baldocchi DD, Hanson PJ. 2001. Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest. *Plant, Cell and Environment* 24: 571–583.
- Zhang X, Friedl MA, Schaaf CB, Strahler AH, Hodges JCF, Gao F, Reed BC, Huete A. 2003. Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment* 84: 471–475.