A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production

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Until recently, continuous monitoring of global vegetation productivity has not been possible because of technological limitations. This article introduces a new satellite-driven monitor of the global biosphere that regularly computes daily gross primary production (GPP) and annual net primary production (NPP) at 1-kilometer (km) resolution over 109,782,756 km² of vegetated land surface. We summarize the history of global NPP science, as well as the derivation of this calculation, and current data production activity. The first data on NPP from the EOS (Earth Observing System) MODIS (Moderate Resolution Imaging Spectroradiometer) sensor are presented with different types of validation. We offer examples of how this new type of data set can serve ecological science, land management, and environmental policy. To enhance the use of these data by nonspecialists, we are now producing monthly anomaly maps for GPP and annual NPP that compare the current value with an 18-year average value for each pixel, clearly identifying regions where vegetation growth is higher or lower than normal.

Keywords: net primary production, MODIS, carbon cycles, terrestrial remote sensing, biosphere

Earth systems science—the integrated analysis of the atmosphere, oceans, cryosphere, and biosphere as a functioning system—had its origins in the early 1980s. A few years earlier, the introduction of the now famous atmospheric "Keeling curve" for carbon dioxide (CO_2), measured at Mauna Loa, Hawaii, had shown definitively for the first time that humans were progressively changing Earth's total atmosphere (Keeling et al. 1976). Atmospheric scientists had recently completed the first primitive global models of atmospheric circulation. Ocean and cryospheric scientists were taking measurements of ocean temperature and ice sheet area, which, although not global, were certainly regional in scope. Unfortunately, however, ecologists (including the senior author) had no background in addressing ecology at global scales. Before the 1980s, biology focused on the organism level, and ecological studies, at best, embraced a 0.1-hectare (ha) field plot. No global ecological measurement was even considered, so analyzing seasonal trends in atmospheric CO_2 concentrations was the only option for assessing global biospheric activity. In early discussions, ecologists considered measuring vegetation density, canopy height, plant biomass, species classes, and other common ecological variables. Only slowly, by realizing that true global measurements could only be made using satellite remote sensing, did ecologists begin to develop a conceptual basis for computing a satellite-based estimate of net primary production (NPP).

From a theoretical standpoint, NPP marks the first visible step of carbon accumulation; it quantifies the conversion of atmospheric CO_2 into plant biomass. The earliest attempts to evaluate ecosystem processes such as NPP at a global scale were made by geographers, and the famous estimates by Lieth and Whittaker (1975) of global NPP are still quoted today. These estimates were based on regressions of temperature data from about a thousand weather stations, computed to a simple annual measure of actual evapotranspiration (AET) in millimeters (mm) per year and then regressed against a handful of NPP field plots. The resulting equation,

$$NPP = 3000\{1 - \exp[-0.0009695(AET - 20)]\},$$

was used to compute and map the first global estimate of NPP (118 billion metric tons per year of biomass) from essentially transformed and coarsely extrapolated meteorology data.

Three activities that first evolved in the early 1980s proved to be the foundations of global-scale terrestrial ecology. First,

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the expansion of atmospheric flask sampling to many additional sites made it possible to draw inferences on a biospheric scale about the photosynthetic uptake of CO_2 in summer, and the evolution of CO_2 in winter, in the Northern Hemisphere (Tans et al. 1990). Second, the global climate models began including simple submodels of land surface processes that incorporated some basic ecology (e.g., physiological controls by stomata on leaf gas exchange; structural vegetation measures such as leaf area index [LAI]). The biosphere-atmosphere transfer scheme, or BATS (Dickinson 1996), laid the foundation for all future representations of terrestrial vegetation in global climate models, such as the well-known SiB (simple biosphere) model of Sellers and colleagues (1986). Third, a few ecologists, most notably Compton J. Tucker of the National Aeronautics and Space Administration (NASA), began exploring data from meteorological satellites (i.e., AVHRR, or Advanced Very High Resolution Radiometer) to see whether some measure of vegetation was discernible. The cover of *Science* in August 1985 inaugurated global vegetation analysis, showing the first NDVI (normalized difference vegetation index) image of the African continent (Tucker et al. 1985).

In the early 1980s, the Reagan administration discouraged NASA from using the fledgling Earth remote sensing only for applications like crop yield analysis (the AgriStars and Lacie programs begun in the 1970s), urging that the technology be used to pursue more "big science" projects. These Reagan administration policies encouraged NASA to begin a new focus on global ecology. Early workshops were brainstorming sessions on "land-related global habitability science issues" (NASA 1983), exploring what kind of ecology could possibly be accomplished globally. It was not long before some initial exploration correlated the annual time series of NDVI to annual NPP, the first step in translating the radiometric index of NDVI to a real ecosystem variable (Goward et al. 1985). Analysis of growing-season dynamics, relating 7-day composites of NDVI to simulations of weekly photosynthesis and transpiration, showed the potential for satellite remote sensing to follow ecosystem canopy processes (Running and Nemani 1988). In the mid-1980s, there were still almost no continuous field measurements of evapotranspiration and photosynthesis; early models of ecosystem biogeochemistry were the only source of information on continuous trends in ecosystem carbon exchange. The late 1980s saw the first ecosystem models driven by remote sensing, operated over a few thousand square kilometers (Running et al. 1989, Burke et al. 1991).

From these beginnings, ecologists have struggled to define and produce a consistent monitor of the terrestrial biosphere, equivalent to the daily weather observations that help develop and test meteorological theory or to the river gauging that serves a similar function for the hydrologic community. Ecologists have sought a repeatable, consistent measurement of the global terrestrial ecosystem that would integrate ecosystem dynamics spatially across Earth's surface (Schimel 1995). This article presents the latest effort to assemble a terrestrial

biospheric monitor, a satellite-derived measure of weekly gross primary production (GPP) from vegetation, which can be composited and expressed to provide an estimate of global annual NPP. Although other articles on global primary production have been published (Prince and Goward 1995, Field et al. 1998), they were based on individual research projects, not on products derived from a continuing and expanding standardized data set. The calculations presented here are executed across the entire vegetated land surface every day and distributed globally every 8 days within 2 to 3 days of acquisition. Although the NASA Earth Observing System (EOS) Terra satellite used for these calculations was launched in December 1999, this data set only began dependable production in mid-2002. The MODIS (Moderate Resolution Imaging Spectroradiometer) sensor is used for the spectral reflectances of terrestrial vegetation used for this research. We briefly summarize the algorithm and processing details, describe current validation efforts, and provide some examples of the scientific value and practical applications of the new products.

Theoretical basis of the algorithm for global NPP

The derivation of a satellite estimate of terrestrial NPP has three theoretical components: (1) the idea that plant NPP is directly related to absorbed solar energy, (2) the theory that a connection exists between absorbed solar energy and satellite-derived spectral indices of vegetation, and (3) the assumption that there are biophysical reasons why the actual conversion efficiency of absorbed solar energy may be reduced below the theoretical potential value. We will briefly consider each of these components.

Relating NDVI, APAR, GPP, and NPP. The original logic of John L. Monteith (1972) suggested that the NPP of well-watered and fertilized annual crop plants was linearly related to the amount of solar energy the plants absorbed over a growing season. This logic combined the meteorological constraint of available sunlight reaching a site with the ecological constraint of the amount of leaf area absorbing the solar energy, while avoiding many complexities of canopy micrometeorology and carbon balance theory. Measures of absorbed photosynthetically active radiation (APAR) integrate the geographic and seasonal variability of day length and potential incident radiation with daily cloud cover and aerosol attenuation of sunlight. In addition, APAR implicitly quantifies the amount of leafy canopy that is displayed to absorb radiation (i.e., LAI). A conversion efficiency, ε, translates APAR (in energy units) to final tissue growth, or NPP (in biomass). GPP is the initial daily total of photosynthesis, and daily net photosynthesis (PSN_{net}) subtracts leaf and fine-root respiration over a 24-hour day. NPP is the annual sum of daily net PSN minus the cost of growth and maintenance of living cells in permanent woody tissue.

Sellers (1987) showed that APAR could be estimated from remote sensing. Spectral vegetation indices derived from remotely sensed data have several forms (Huete et al. 2002); the most widely applied currently is NDVI, which is calculated

from surface reflectance in red and near-infrared (NIR) wavelengths as

$$NDVI = (NIR - red)/(NIR + red)$$

and

$$APAR/PAR \approx NDVI,$$

where PAR is the incident radiation in photosynthetic wavelengths (in megajoules). Consequently, spectral vegetation indexes such as NDVI most directly quantify the fraction of photosynthetically active radiation (FPAR) that is absorbed (ranging from 0 to 1):

$$FPAR = APAR/PAR \approx NDVI.$$

FPAR and LAI are combined into a MODIS land surface variable that is computed daily and composited at 8-day intervals (Myneni et al. 2002). When FPAR, derived from a spectral vegetation index, is multiplied by daily incident radiation (PAR, in megajoules per square meter) and the conversion efficiency (ε, in grams [g] of carbon per megajoule),

$$GPP = \varepsilon \times FPAR \times PAR \approx \varepsilon \times NDVI \times PAR.$$

An intermediate variable of daily net photosynthesis, PSN_{net}, is computed as

$$PSN_{net} = GPP - R_{lr},$$

where R_{lr} is 24-hour maintenance respiration of leaves and fine roots.

The annual NPP is

$$NPP = \Sigma (PSN_{net}) - R_g - R_m,$$

where R_g is the annual growth respiration required to construct leaves, fine roots, and new woody tissues, and R_m is the maintenance respiration of live cells in woody tissues (Running et al. 2000). Combined, these simple relationships derived from a satellite radiometric index, vegetation canopy reflectance properties, and CO_2 fluxes provide the basis for scientists to use remote sensing to extrapolate carbon cycle processes globally.

Biophysical variability of ε. The PAR conversion efficiency, ε, varies widely with different vegetation types (Field et al. 1995, Prince and Goward 1995, Turner et al. 2003a). There are two principal sources of this variability. First, with any vegetation, some photosynthesis is immediately used for maintenance respiration. For the annual crop plants from the original theory of Monteith (1972), these respiration costs were minimal, so ε was typically around 2 g carbon per megajoule. Respiration costs, however, increase with the size of perennial plants. Hunt (1994) found that published ε values for woody vegetation were much lower, from about 0.2 to 1.5 g carbon

per megajoule, and hypothesized that this was the result of respiration from the 6% to 27% of living cells in the sapwood of woody stems (Waring and Running 1998).

The second source of variability in ε is attributed to suboptimal climatic conditions. To extrapolate Monteith's original theory, designed for well-watered crops only during the growing season, to perennial plants living year-round, certain severe climatic constraints must be recognized. Evergreen plants such as conifers absorb PAR all during the nongrowing season, yet subfreezing temperatures stop photosynthesis, because leaf stomata are forced to close (Waring and Running 1998). As a global generalization, the algorithm truncates GPP on days when the minimum temperature is below –8 degrees Celsius (°C). High vapor pressure deficits, or VPDs (> 2000 pascals), have also been shown to induce stomatal closure in many species. This level of daily atmospheric water deficit is commonly reached in semiarid regions of the world for much of the growing season. Our algorithm mimics this physiological water stress control, progressively limiting daily GPP by reducing ε when high VPDs are computed from the surface meteorology. We also assume nutrient constraints on vegetation growth to be quantified by limiting leaf area, rather than attempt to compute a constraint through ε. This assumption is not entirely accurate, as ranges of leaf nitrogen and photosynthetic capacity occur in all vegetation types (Schulze et al. 1994). Spectral reflectances are somewhat sensitive to leaf chemistry, so the MODIS-derived FPAR and LAI may represent some differences in leaf nitrogen content, but in an undetermined way.

To quantify these biome- and climate-induced ranges of ε, we simulated global NPP in advance with a complex ecosystem model, Biome-BGC (biome biogeochemical cycles), and computed the ε, or conversion efficiency, from APAR to final NPP. The resulting biome parameter look-up table, or BPLUT, contains parameters for temperature and VPD limits as well as specific leaf area and respiration coefficients for representative vegetation in each biome type (Running et al. 2000, White et al. 2000). Only very general biome types are defined, such as evergreen needleleaf forest, deciduous broadleaf forest, shrubland, savanna, grassland, and cropland. The BPLUT also defines biome differences in carbon storage and turnover rates.

Global surface meteorology. The NASA Data Assimilation Office (DAO) collects data from all available surface weather observations globally every 3 hours. The DAO then interpolates and grids these point data, runs a global climate model on a short time sequence, and produces an estimate of climatic conditions for the world, at 10 meters above the land surface (approximating canopy height conditions) and at a resolution of 1° by 1.25°. From these data, the MODIS NPP algorithm retrieves four measurements: (1) average 24-hour daily temperature (°C), (2) daily 24-hour minimum temperature (°C), (3) actual vapor pressure (derived from DAO specific humidity, in pascals), and (4) incident shortwave solar
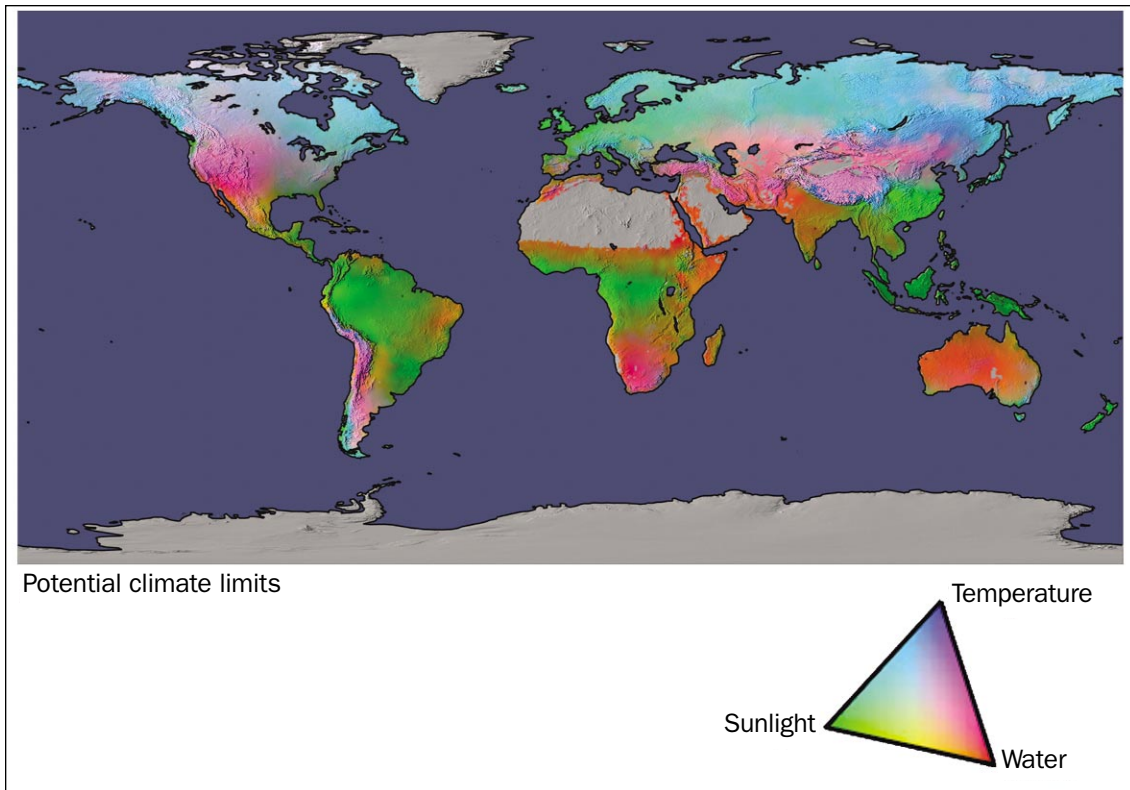
Figure 1. Analysis of the geographic variation in climatic controls of terrestrial net primary production from water, temperature, and radiation limitations. Data are from Nemani and colleagues (2003).

radiation (megajoules per square meter per 3-hour time step). GPP is then computed daily for each 1-square-kilometer (km) pixel with these meteorological data.

Availability and retrieval of global NPP data. Each day, a data system known as EOSDIS (Earth Observing System Data Information System) computes calibrated and atmospherically corrected reflectances from each spectral channel of the MODIS sensor for each cloud-free pixel. To make the daily GPP computation for each global terrestrial pixel, three other variables must first be retrieved: (1) the biome type, which is recomputed annually; (2) the FPAR, which can change weekly during rapid vegetation growth and senescence; and (3) the daily surface climate conditions, which change diurnally.

The final global GPP is computed daily and summed every 8 days for 109,782,756 km^2 of vegetated land area at 1-km spatial resolution. The file to produce this global data set is 2.1 gigabytes in the standard EOS data format, but it can be reduced substantially by translating it into different resolutions and projections. NASA's current policy is that global EOS data sets such as those for GPP and NPP will be available to the international scientific community at no more than the cost of reproduction. The NPP data set is archived and distributed from a NASA-authorized data center within 2 to 3 days of the end of each 8-day computational period (Justice et al. 2002). Full details of the EOS GPP and NPP data avail-

ability, and of the algorithms and processing associated with the data, can be found at *www.ntsg.umt.edu/.*

Controls and historic trends of global NPP

Figure 1 gives a sense of the climatic controls and range of global annual NPP, distributed from arctic tundra to tropical rain forests. Water is the factor that limits NPP most strongly on 40% of the land surface, including regions with negative water balances as low as −3000 mm per year (figure 2). Temperature is the strongest limiting factor on 33% of the land surface, with annual temperature ranges from −20°C in arctic tundra to 30°C in deserts. Incident solar radiation is the primary limiting factor in 27% of global vegetated areas, mostly in wet tropical regions where temperatures and water availability are usually adequate (Nemani et al. 2003). While it is easy to imagine boreal areas being temperature limited and deserts being water limited, partial constraints limit the NPP of temperate regions in a complex fashion at different times of the growing season. A temperate mid-latitude forest may be limited by radiation and temperature in winter, by temperature in spring, and by water in midsummer.

Applying the MODIS NPP algorithm to AVHRR satellite data, Nemani and colleagues (2003) evaluated recent trends in global NPP from 1982 through 1999. The somewhat surprising result is that overall global NPP increased by 6.2% during this period, with 25% of global vegetated area showing significant increases and only 7% showing decreasing trends. The

complex geographic pattern of these trends (figure 3) illustrates that the Amazon basin accounted for 42% of the increase in global NPP. These trends in NPP are a biospheric response to recent changes in global climate, including higher temperatures, longer temperate growing seasons, more rainfall in some previously water-limited areas, and increased radiation (a result of reduced cloudiness) in regions such as the Amazon basin. Other analyses of the AVHRR NDVI satellite record from 1982 through 1999 for North America have also shown increases in NPP in certain regions (Hicke et al. 2002, Nemani et al. 2002). Alaska and northwestern Canada showed a trend of higher spring temperatures and longer growing seasons; the Midwest agricultural region and New England forests showed higher midsummer NPP correlated with increased precipitation; and the southeastern forests showed longer growing seasons in the fall, optimized by replacing deciduous hardwoods with evergreen pine trees.
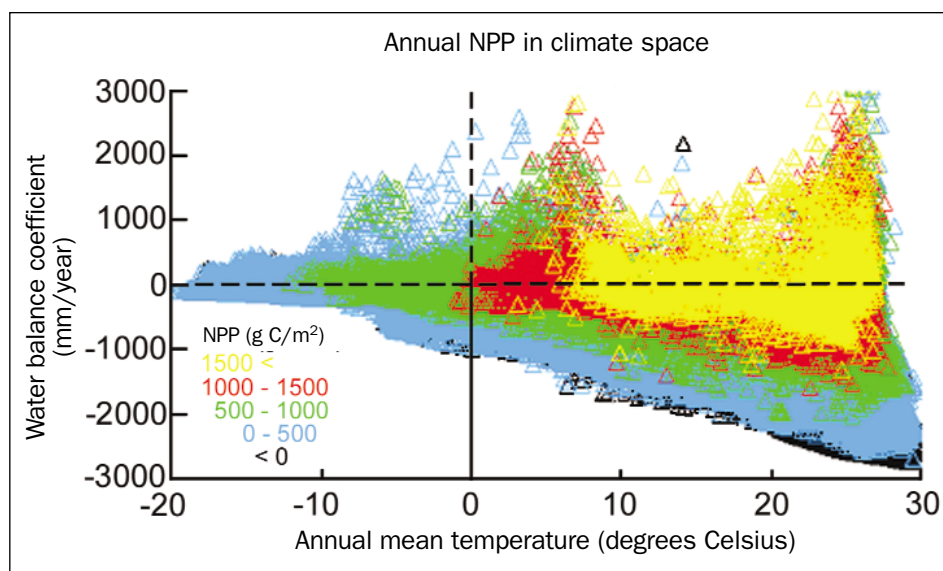

Figure 2. Model of simulated global annual net primary production (NPP) mapped in climate space to show the general range of water availability and temperatures where NPP exists. Modified from Churkina and Running (1998).

Nemani and colleagues (2003) compared the interannual variability of satellite-computed annual NPP with time series of atmospheric CO_2 anomalies. Although we would expect increases in NPP to decrease atmospheric CO_2 by increasing
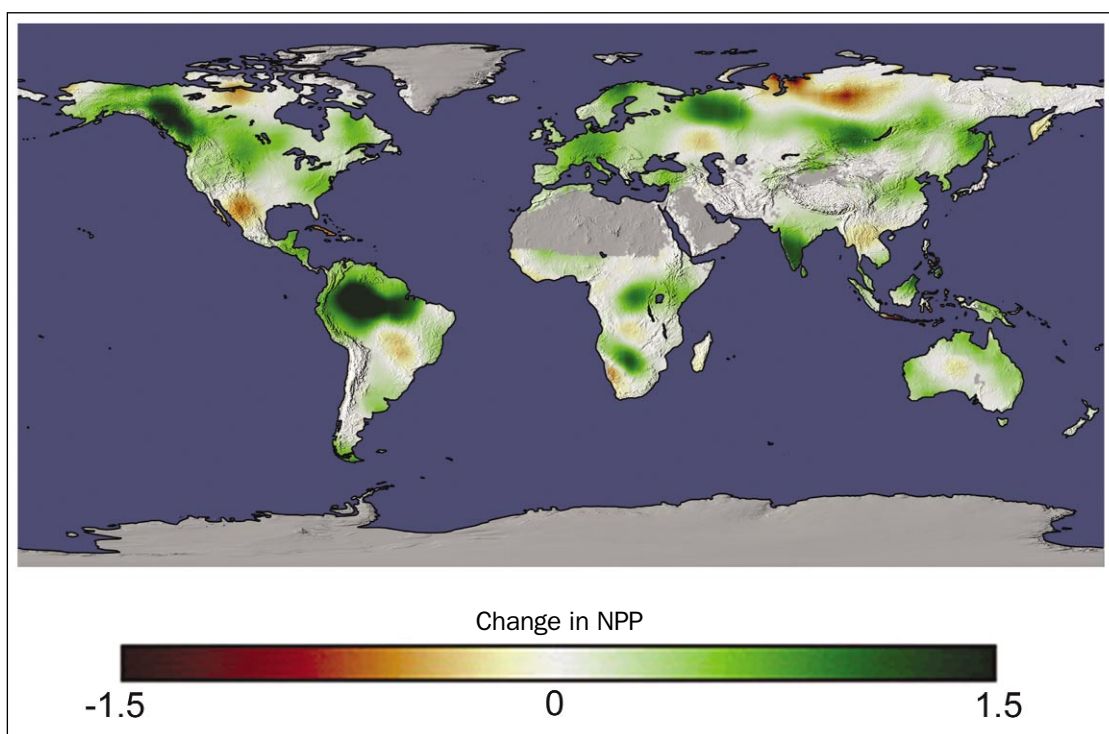

Figure 3. Trends in global net primary production (NPP) anomalies from 1981 through 1999, computed from the historical AVHRR-NDVI (Advanced Very High Resolution Radiometer–normalized difference vegetation index) data set. Data are from Nemani and colleagues (2003).
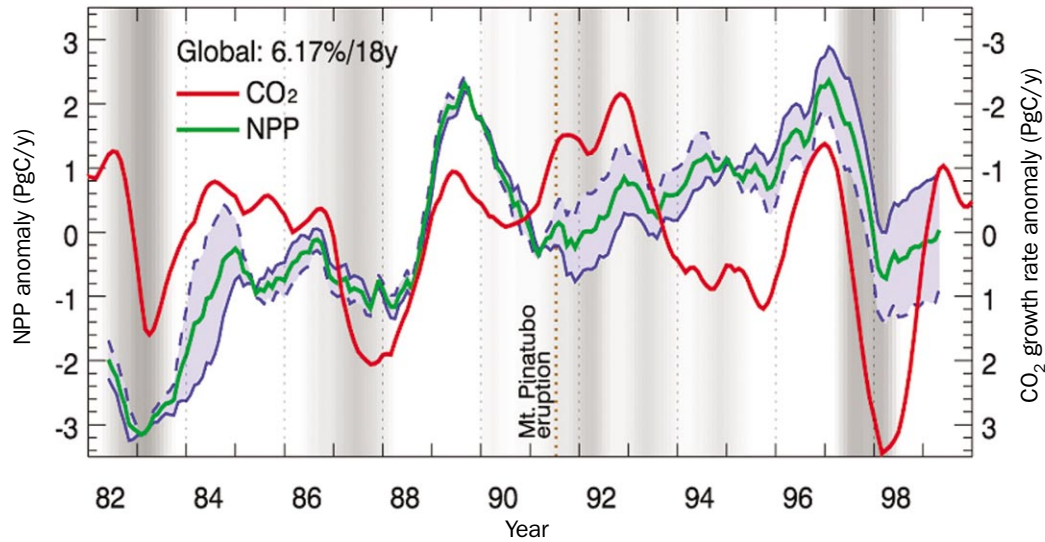
Figure 4. Relationship between the interannual anomaly of global net primary production (NPP) from the MODIS (Moderate Resolution Imaging Spectroradiometer) NPP algorithm and data on atmospheric carbon dioxide (CO_2) concentration, using AVHRR-NDVI (Advanced Very High Resolution Radiometer–normalized difference vegetation index) data from 1981 to 1999 (Nemani et al. 2003). Note that the CO_2 anomaly axis is inverted to align the NPP and CO_2 trends.

photosynthetic uptake, NPP does not include the CO_2 released by heterotrophic respiration. The NPP anomaly from 1982 through 1999 was inversely correlated to the atmospheric CO_2 anomaly, with an *r* of 0.70 (figure 4). The atmosphere mixes CO_2 sources and sinks with time dynamics somewhat shorter than the 8-day MODIS GPP, but it integrates a spatial area much larger than a 1-km pixel, making interpretations of these correlations difficult.

Validation of the MODIS daily GPP and annual NPP

Validation of a new global data set is daunting, as ideal testing would include measuring daily GPP and annual NPP across a full range of biome types and climates. An algorithm that is successful in a boreal needleleaf forest may be inadequate in a tropical rain-green savanna. Consequently, a global array of validation sites is needed (Morisette et al. 2002). More fundamentally, every measure available to validate GPP and NPP represents a different spatial scale and presents different limitations (Running et al. 1999). Three types of data seem useful for validating global GPP and NPP data: direct measurements of biomass, tower flux measurements, and measurements of atmospheric CO_2 concentration. However, each type of data is limited in its precision or scope. Direct biomass measures of NPP often are only annual, and the sample area is usually less than 1 ha. Tower flux measurements are continuous in time and sample a "footprint" near the MODIS 1-km pixel size, but the flux towers directly measure only net ecosystem exchange (NEE), so NPP and GPP must be derived from carbon balance principles. Measurements of atmospheric CO_2 concentration integrate a large, somewhat undefined land area and include anthropogenic CO_2 emissions, but they are gathered in an

instantaneous sampling process that is repeated only monthly. In short, no single measure can match the detail that the MODIS GPP and NPP represent in terms of time, space, and ecosystem attributes. We must therefore employ a set of multiple estimations to define realistic values for daily GPP and annual NPP in time and space.

Ecologists have measured annual NPP through direct sampling of biomass growth increment for decades. Recently, intensive efforts have been made to compile all credible published estimates of terrestrial NPP (Clark et al. 2001, Scurlock and Olson 2002, Zheng et al. 2003). Scurlock and Olson (2002) found the known range of NPP for temporal and boreal biomes to be 20 to 1160 g carbon per square meter per year. Clark and colleagues (2001) estimated that the NPP for tropical forests ranged from 170 to 2170 g carbon per square meter per year. This range of two orders of magnitude in field-measured NPP reflects the large global climatic gradients in temperature and water availability constraining NPP (figure 2). Interannual variability in NPP also reflects these strong climatic constraints. Knapp and Smith (2001) found a range of aboveground NPP from 116 to 744 g carbon per square meter per year across 11 US LTER (Long Term Ecological Research) sites, ranging from arctic tundra to grasslands and deciduous forests. Moreover, in evaluating a decade or more of annual NPP from these sites, they discovered that interannual variability of 20% to 30% was common as the vegetation responded to normal year-to-year variation in precipitation and temperature. We estimate a global annual NPP for 2001 of 57.7 petagrams (Pg) carbon, an average of 509 g carbon per square meter, and an NPP for 2002 of 55.5 Pg carbon, or 489 g carbon per square meter of vegetated land (figure 5).
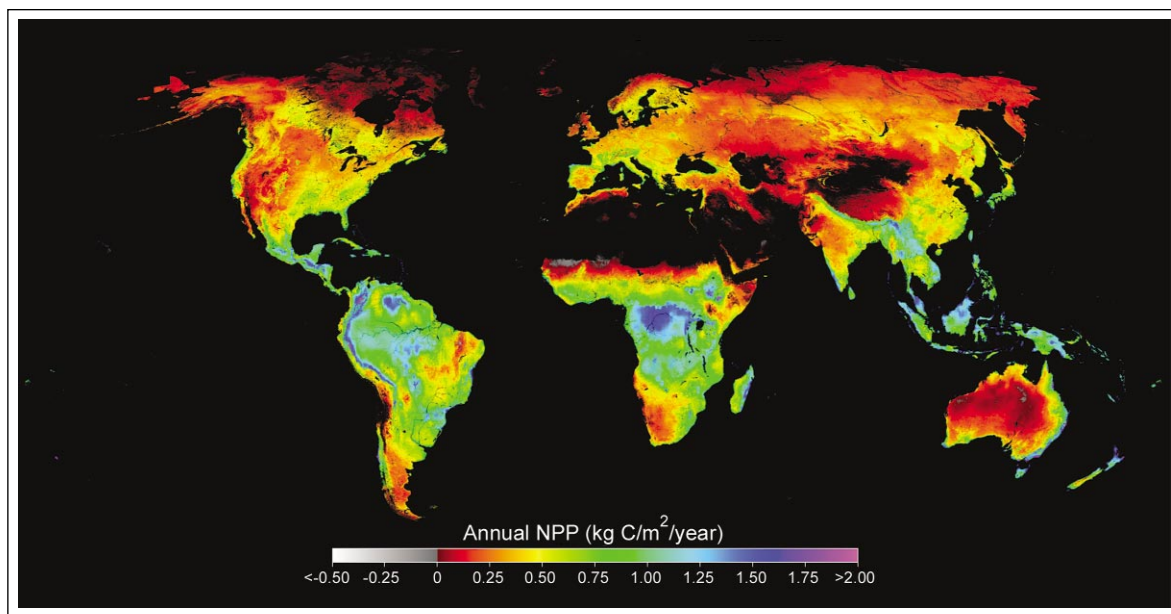
Figure 5. Global terrestrial net primary production (NPP) over 110 million square kilometers for 2002, computed from MODIS (Moderate Resolution Imaging Spectroradiometer) data.

For a more refined test, we checked the range and distribution of NPP produced for different biome types in 2002 (figure 6). The range of MODIS NPP for evergreen needleleaf forests was 150 to 900 g carbon, with a mean of 451 g carbon per square meter per year, close to the mean of 432 g compiled from field data by Zheng and colleagues (2003). Zheng and colleagues found a mean NPP for temperate broadleaf deciduous forests of 635 g carbon, in comparison with the mean of 492 g from our MODIS data set. MODIS estimates of tropical evergreen broadleaf NPP averaged 1218 g carbon per square meter, with a range from 400 to 1800 g. In field measurements of NPP for tropical forests, Clark and colleagues (2001) estimated an NPP ranging from 170 to 2170 g carbon, using extensive measurements from 39 sites. Grassland NPP ranged from 70 to 410 g carbon, with a mean of 203 g, in Zheng and colleagues' (2003) data set. The MODIS grassland NPP, by comparison, showed a mean of 254 g carbon and a maximum of 750 g. These initial comparisons indicate that the MODIS computations of NPP fall within the ranges of existing field data.

Beginning in the early 1990s, scientists organized by the International Geosphere-Biosphere Programme planned an international network of eddy covariance flux stations that would continuously measure CO_2, water, and energy exchange from representative ecosystems (Baldocchi et al. 2001). This network, now called FLUXNET, includes more than 200 tower sites spanning all continents and biome types and providing accurate seasonal measures of vegetation carbon uptake and local land CO_2 balances (Falge et al. 2002). To test the MODIS 8-day GPP, we provide researchers from
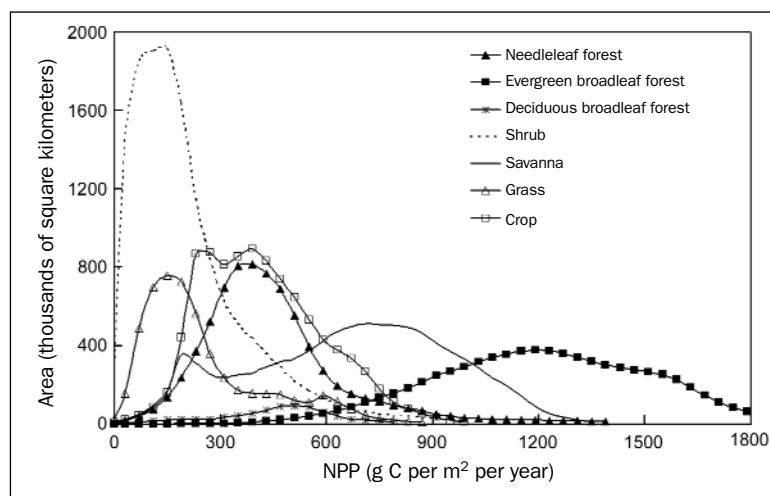

Figure 6. Global areal distribution of terrestrial net primary production (NPP) for 2002 by simple biome types (see figure 5).

the AmeriFlux network (*http://public.ornl.gov/ameriflux/*) with estimates of GPP to compare with flux tower–based meteorological data and GPP estimates for 2001. Every 8 days, a window of the MODIS daily GPP (7 by 7 pixels) is retrieved at the exact location of these towers, and we make a direct comparison between the MODIS GPP and tower measurements of vegetation GPP (figure 7). This protocol is being expanded to all global FLUXNET sites in 2004 (see *http://daacl.esd.ornl.gov/FLUXNET/*).

Inputs to the algorithm included LAI and FPAR estimates from MODIS and the most recent version of the DAO global meteorology data set The results indicate that the MODIS algorithm captures the seasonality of site daily GPP quite well across a wide array of climates (figure 7). From the earliest
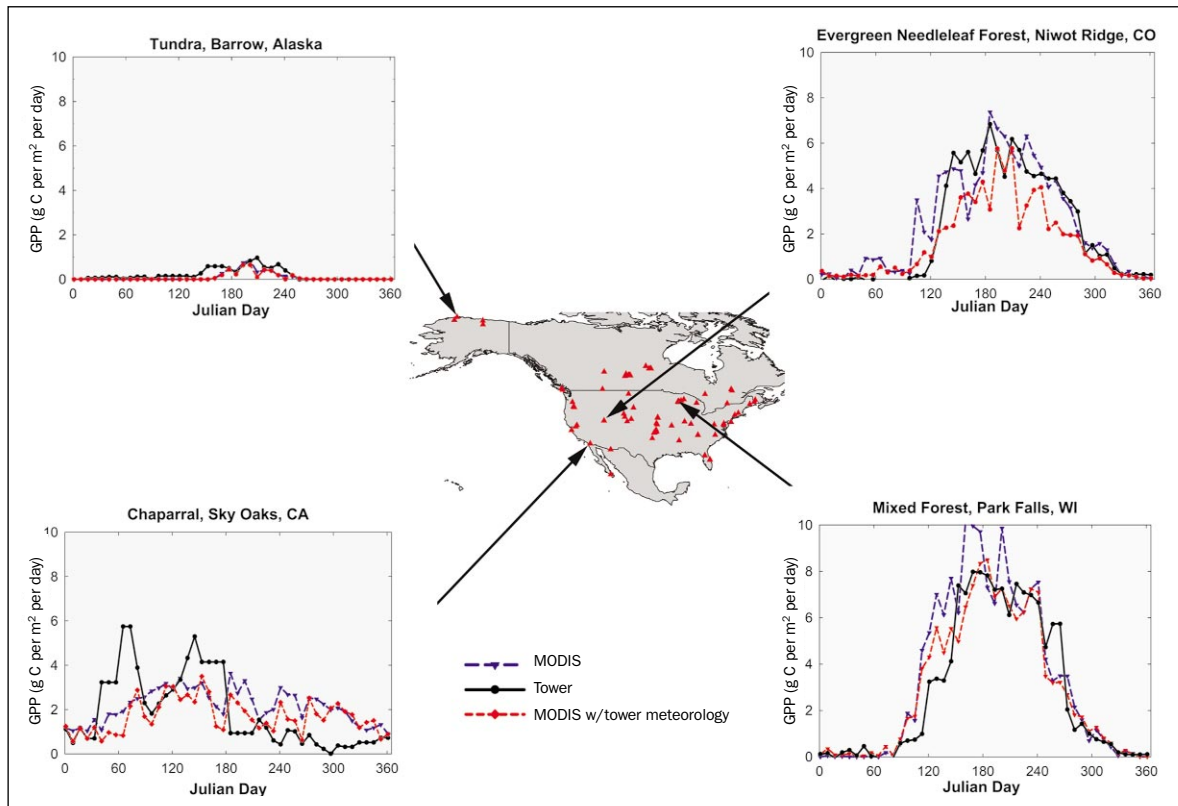
Figure 7. Intercomparison of gross primary production (GPP) computed from daily MODIS (Moderate Resolution Imaging Spectroradiometer) data summed at 8-day intervals with GPP measurements from flux towers at sites in the AmeriFlux network that represent different biomes and climatic regimes for 2001. Substituting higher-resolution (1 to 5 km) daily local tower meteorology data for the lower-resolution (1° by 1.25°) global meteorology data in a replicated calculation of GPP allows separation of error sources in the MODIS algorithms.

studies with NDVI, it has been evident that these satellite data do well at quantifying the length of the growing season, estimated as the number of days per year that green leaf area is displayed (Running and Nemani 1988, Myneni et al. 1997).

The MODIS algorithm appears to underestimate the initial burst of springtime GPP, yet it also consistently overestimates midsummer GPP, because of insufficient drought constraints for some of the biomes studied. To estimate the effects of the global meteorology data on algorithm results, tower data were then substituted for the DAO global meteorology data, and the MODIS GPP algorithm was recalculated. Our analysis indicates that much of this overestimation of daily GPP is a result of the discrepancy between global and tower meteorology data created by their spatial disparity. The global meteorology data are provided at a resolution of 1° by 1.25°, whereas the tower meteorology data represent a much smaller area (approximately 1 to 5 km²). The primary difference between the two data sets is found in the VPD values. The VPD from global meteorology is consistently lower than tower VPD because of area averaging, resulting in increasingly erroneous estimates of GPP as a site dries (figure 7). The use of tower meteorology with the MODIS GPP algorithm usually improves GPP comparisons with tower results, indicating

that the logic used in the MODIS algorithm is sound across biome types.

Additional errors propagate from the MODIS LAI/FPAR data set, in which cloud contamination is often an issue, leading to erroneously low estimates of LAI and producing data noise within the 8-day average GPP. This cloud contamination problem occurs most often in boreal and tropical regions but is also evident periodically throughout the United States. Biome-BGC estimates of GPP that incorporate a full mechanistic calculation of carbon balance are being used to explore other reasons for the differences between tower and MODIS estimates of daily GPP (Thornton et al. 2002, Turner et al. 2003b).

Sources and sinks of CO_2 are quantified by NEE, which is related to NPP on an annual basis as

$$NEE = NPP - R_h,$$

where R_h is the heterotrophic respiration or decomposition of biomass, primarily in the soil. This additional carbon cycle process is exceedingly difficult to quantify over large areas. NEE can range from 10% to 50% of NPP, depending on the soil carbon pools available for decomposition

(Baldocchi et al. 2001, Falge et al. 2002). NEE is measured directly by eddy covariance flux towers, and additional field measurements are taken to partition it into the components of NPP and soil respiration. Consequently, the MODIS NPP provides a critical first step for computing NEE globally, but additional modeling steps are required to compute the global NEE estimate (Schimel 1995, Potter 1999).

Satellite data are frequently combined with inversion of atmospheric CO_2 data to provide a constraint on global modeling of the CO_2 balance (Randerson et al. 1997). Using this technique, Schaefer and colleagues (2002) concluded that 44% of global interannual variability in NEE resulted from precipitation patterns, 23% from LAI, 16% from temperature, and 12% from soil carbon. Their study from 1983 to 1993 was limited by using monthly NDVI data at 1° by 1° resolution, whereas future studies will be able to use MODIS data on GPP distributed every 8 days at 1-km resolution.

Scientific applications of MODIS GPP and NPP

A continuously computed and openly disseminated measure of total daily GPP and annual NPP for Earth's land surface has never before existed. As summarized in the previous sections, development of the theory, algorithms, data streams, and validation of a regular measure of GPP and NPP has been an active research topic for the last two decades. Although refinement of this spatially continuous monitoring of the biosphere will continue for many years, we suggest that these GPP and NPP data sets are now sufficiently mature to be used in a wide variety of ways, wherever regular, spatially referenced measures of vegetation activity are desired. This section suggests a variety of applications for science, policy, and land management in which this regular measure of GPP and NPP should be valuable.

The original demand for global-scale land surface data was created by global climate and weather forecasting models, and this demand remains today (Sellers et al. 1986). Future global climate models will require dramatically more detailed definition of vegetation cover and physiology to reach the goal of comprehensive Earth systems models (Schimel 1999, Bonan et al. 2002). New models such as the community climate model at the National Center for Atmospheric Research now use MODIS GPP and NPP data to build algorithms computing seasonal changes in vegetation phenology, leaf area, roughness length, energy partitioning, and CO_2 source-sink relationships. Other greenhouse gases are also important as land surface feedbacks to the atmosphere for global climate modeling. Methane and nonmethane hydrocarbons (NMHCs) are thought to produce 20% to 30% of the current greenhouse gas forcing in the atmosphere (Houghton et al. 2001). Global methane and NMHC emissions can be calculated as a fraction of global NPP on the basis of biome type and temperature, providing reasonable spatial distribution and seasonal activity (Potter et al. 2001).

Because NPP is an essential component of the carbon cycle, virtually any science question involving the biospheric support of humankind begins by assessing NPP. The most

fundamental questions of environmental degradation—desertification, deforestation, and the impacts of pollution and climate change—are often addressed by evaluating changes in NPP. Understanding differences in NPP among different biomes in different bioclimatic regimes is critical in defining a baseline of healthy biospheric function by which to measure future degradation. The Kyoto protocol on greenhouse gases focuses on the sources and sinks of CO_2 that begin with the NPP of terrestrial systems. Because NPP has natural interannual variability of 20% to 30%, regular monitoring may provide the most defensible estimations of CO_2 balance.

Natural disturbances such as wildfire also change the NPP over a total area of 1 million to 8 million km^2 per year, an estimate made with very little confidence. Human conversions of vegetation also change the NPP over millions of square kilometers each year. Deforestation rates are best quantified by methods of detecting land-cover change that automatically record abrupt changes in vegetation reflectance, signifying a severe disturbance such as deforestation (Zhan et al. 2002). The recovery of a site from a disturbance, however, is rarely followed so carefully, and measurement of such recovery may best be accomplished with the MODIS NPP data.

Biodiversity is commonly described as a measure of ecosystem health, yet at a global scale it is unquantifiable. Sala and colleagues (2000) defined five major drivers for change in global biodiversity in the next century: land use, climate, nitrogen deposition, biotic exchange, and atmospheric CO_2 increase. Although global NPP cannot count species, it integrates the biospheric response of all five of these primary drivers. Consequently, biodiversity has long been related in various ways to NPP. However, different biomes, bioclimatic regimes, disturbance histories, and other factors prevent a straightforward assessment of the relationship between NPP and biodiversity. Waring and colleagues (2002) recently suggested that biodiversity may be highest at sites with intermediate levels of NPP. Sites with high NPP often are dominated by relatively few fast-growing species, while sites with low NPP have insufficient resources to support a variety of species. Waring and colleagues found that a ratio of spring to summer photosynthesis best quantified the intermediate productivity. This ratio was easily calculated for the entire state of Oregon from AVHRR NDVI data and can now be computed directly from the MODIS 8-day GPP data stream (figure 8).

Estimates of NPP are often used as the beginning point of socioeconomic analyses of biomass utilization. For example, Haberl and Geissler (2000) used satellite data to produce a georeferenced map of NPP for Austria. They found that 50% of Austria's NPP was being appropriated by humans for food and fiber products (including forest and crop residues). Further, Haberl and Geissler estimated from a cascade utilization logic that unused biomass residues could fulfill 6% of Austria's commercial energy demand if they were fully utilized.

Terrestrial NPP is regularly identified as a key variable for various ecological monitoring activities (Niemeijer 2002). The Environmental Sustainability Index (*www.ciesin.*
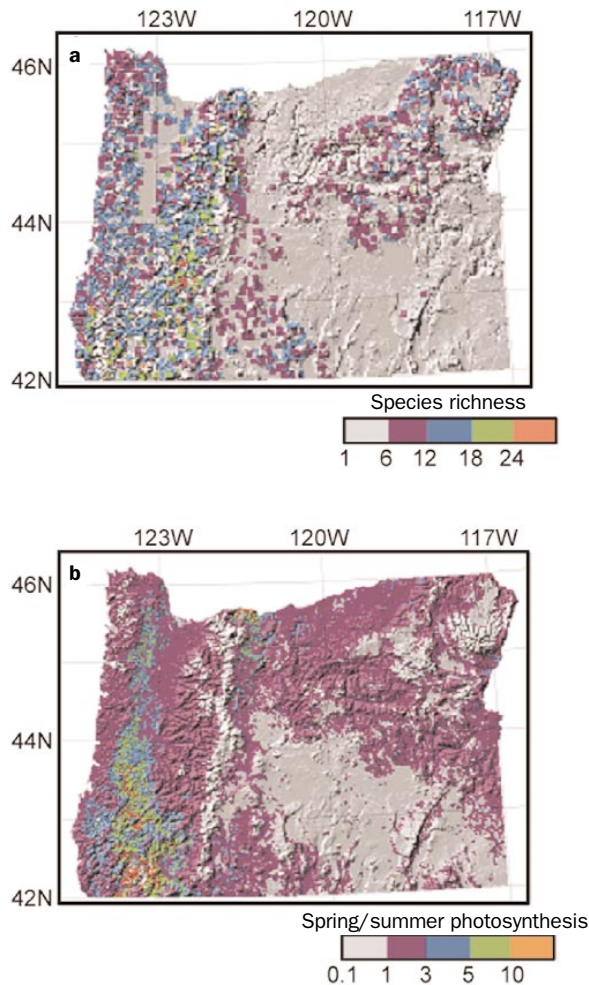
Figure 8. Testing an index of woody species biodiversity for Oregon. (a) Richness of woody species measured at field plots. (b) Ratio of spring (March–May) to summer (June–August) photosynthesis, computed by Waring and colleagues (2002) from a satellite-driven gross primary production (GPP) model. Biodiversity appears to be higher in areas with high ratios of spring to summer photosynthesis, a calculation easily performed for large areas with the GPP data gathered by MODIS (Moderate Resolution Imaging Spectroradiometer).

Figure 9. (a) The relationship between scaled aboveground green biomass (kilograms of carbon per square meter) and estimates of gross primary production (GPP), derived from MODIS (Moderate Resolution Imaging Spectroradiometer) data for 2001 and 2002. (b) Observed spring wheat yield for selected counties in Montana. Each point represents a county in Montana with more than 12,000 hectares (ha) of reported dryland-farmed spring wheat in 2001.

columbia.edu/indicators/ESI/) of the World Economic Forum, the Heinz Center's *State of the Nation's Ecosystems* report (*www.heinzctr.org/ecosystems/*), and the National Research Council report *Ecological Indicators for the Nation* (*www.nap.edu/books/0309068452/html/*) all identify NPP as a primary monitoring variable. The greatest interest of these indexes and reports is in quantifying trends of ecological indicators such as NPP and sounding an early alarm if an ongoing degradation is detected in any part of the nation or world. Reaching the overall objective of global sustainable development will require specific measurements of the
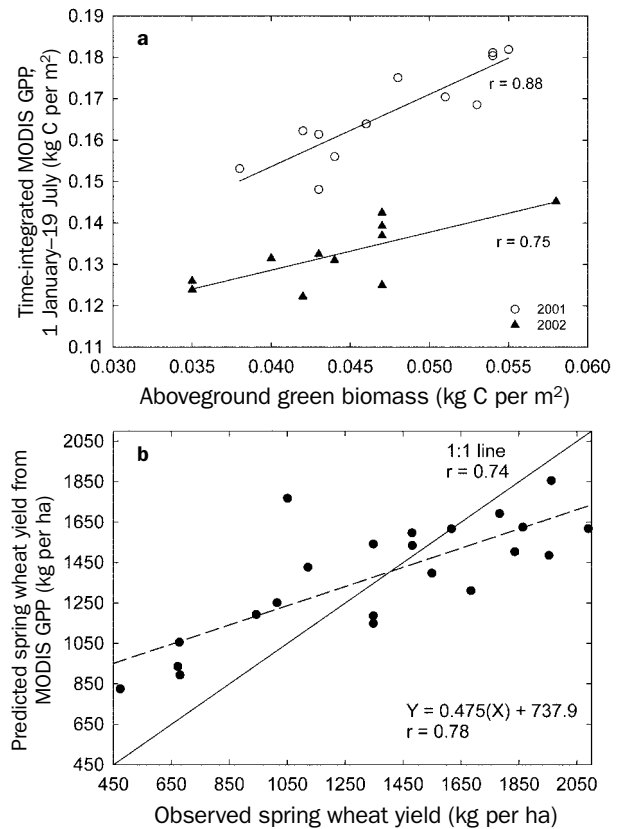
stability of key biosphere attributes (Kates et al. 2001), and documentation of clear degradation in an ecosystem should trigger policy shifts in land management.

Regional landscape planning and management applications

Possible uses of the MODIS data on GPP and NPP range from regional strategic planning, such as quantifying decadal harvest targets for large tracts of forests, to more immediate decisions, such as when to move grazing animals among large pasture areas (Hunt et al. 2003). Immediate data access is not as important for strategic planning as it is for tactical decisionmaking. Strategic planning may use decadal trends in annual NPP as a measure of regional patterns and possible degradation of productive capability. Desertification of sub-Saharan Africa, for example, was long thought to be caused primarily by overgrazing, and substantial international aid was directed toward improving land management practices. Only after precipitation records were correlated
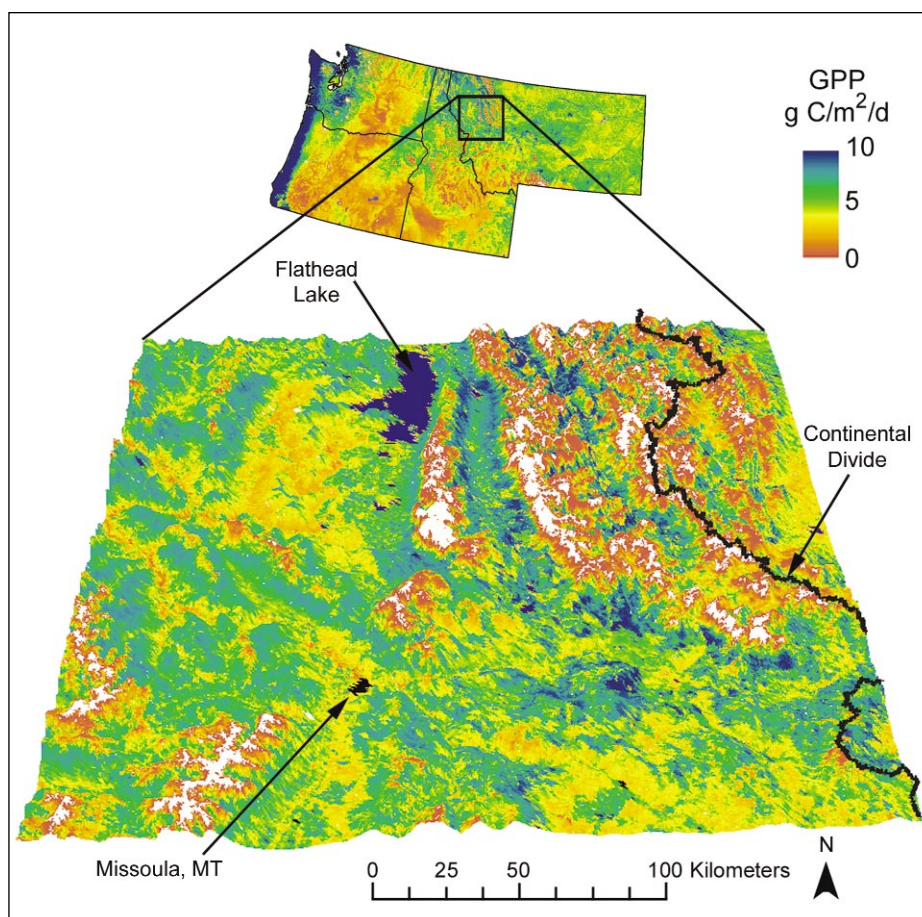
Figure 10. Improvement in landscape resolution that the new 250-meter MODIS (Moderate Resolution Imaging Spectroradiometer) measurement of gross primary production (GPP) attains over the standard global MODIS GPP/NPP (net primary production) data set. The map shows GPP from western Montana for 2–10 June 2003, draped over digital elevation data.

with satellite-based analysis of interannual variability in NDVI on a regional scale was it concluded that most of the apparent degradation was a result of decadal climate trends (Nicholson and Tucker 1998).

Decadal watershed degradation, including erosion and sedimentation, is also a serious land management problem. Local riverbank erosion and sedimentation is easily visible and documented on the ground, but the degradation of vegetation on a regional scale, such as the entire Colorado River basin or the basin of the Rio Grande, can only be quantified by repeated large-scale measurements such as those provided by remote sensing. Available fresh water is becoming possibly the scarcest natural resource; hence, monitoring and forecasting hydrologic runoff will have increasing socioeconomic value (Jackson et al. 2001). Evapotranspiration by vegetation consumes on average 70% of the precipitation that falls, and so computing dynamic runoff requires accurate analysis of vegetation growth.

Tactical decisionmaking on land management can benefit from immediate access to the latest MODIS data. Public land managers must reevaluate grazing schedules as seasonal weather changes the foraging conditions. Setting fixed calendar dates in grazing schedules is inappropriate because interannual weather variability can cause vegetation development to vary widely, and droughts reduce grazing capacities. Reeves (2004) established the relationship between MODIS GPP estimates and regional vegetation conditions during the 2001 and 2002 growing seasons. In his study, herbaceous vegetation was clipped at 2200 plots in the Little Missouri National Grasslands in western North Dakota. These field observations were spatially scaled to the zone of local meteorological influence established by creating Thiesson polygons around weather stations within the study area. Field observations compared favorably with MODIS GPP estimates, especially during the peak of greenness and of grass LAI (figure 9a).

The data on NPP gathered by MODIS have strategic and tactical uses for agriculture and agricultural economics. Commodity traders have clear interest in following how crops are growing in competing areas worldwide. The global price
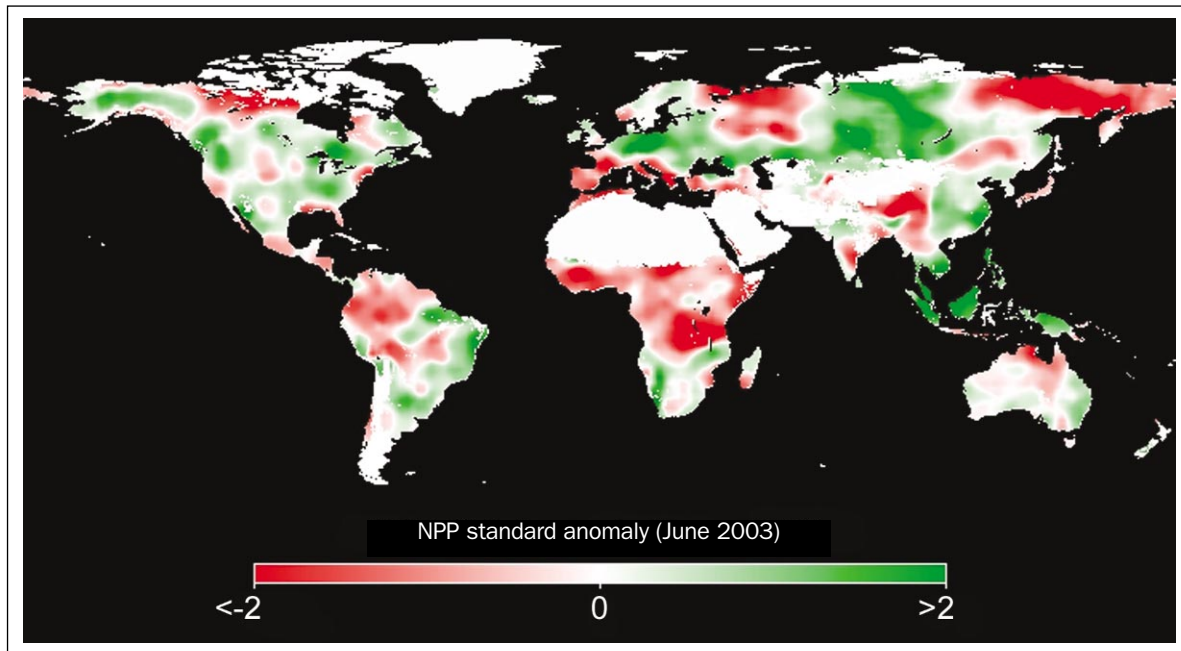
Figure 11. A trend of monthly net primary production (NPP) anomalies for the terrestrial biosphere, derived from the MODIS GPP data and expressed as the departure in standard deviations from the long-term (1982–2003) mean. The anomaly map suggests regional trends in ecosystem health without requiring understanding of carbon cycle details.

of wheat fluctuates in response to information on current crop conditions and expected yields in key exporting countries such as Canada, Argentina, and Australia. Even advance logistical decisions, such as requirements for leasing rail cars to transport crops to markets, can benefit from improved real-time assessments of crop development. Reeves (2004) demonstrated that combining 8-day MODIS GPP estimates with a simplified algorithm for wheat yield was an effective, timely tool for estimating county- and state-level spring wheat yield in Montana, the third largest wheat-producing state in the United States. In that study, GPP estimates were integrated over a defined growing season from 15 April through 4 August 2001 and converted to wheat yield using a simple harvest index (figure 9b).

Crop insurance is a $3-billion-per-year industry in the United States. Insurers need an objective means of evaluating whether an area meets some threshold of crop damage from hail or of retarded development from drought. The MODIS 8-day GPP may provide one means of arriving at decisions as to which farms qualify for insurance payments or for disaster relief from the federal government. At this stage, however, the MODIS NPP data should be considered only a general index of crop development. Until more detailed models are ready that begin with MODIS GPP and add computations of species, and even of cultivar-specific developmental sequences, we will lack the accuracy desired for specific crops and areas.

Wildfire has become the most costly wildland hazard in the United States, with the annual costs of fire suppression exceeding $1 billion in recent years. Sophisticated physical models of fire intensity and behavior now exist to aid in management, but these models require georeferenced databases of wildland fuels, the dead and live biomass that propagates fire spread (Keane et al. 2001). Seasonal development and senescence of the grasses and herbaceous plants that provide initial ignition for fire and promote its spread are being derived from the MODIS 8-day GPP. Postfire recovery of vegetation in burned areas can also be measured with MODIS NPP data.

For satellite data to have value for land management, the resolution must be sufficient to resolve major ownership and ecotonal boundaries. A 0.25-km version of the MODIS GPP and NPP data stream, using 1-km daily surface meteorology, is now being developed for the continental United States to provide a high-resolution GPP and NPP for land management. These products are designed for tactical decisionmaking and thus will be available only 2 to 3 days after the end of each 8-day MODIS compositing period (figure 10). The 0.25-km data set resolves details of vegetation productivity resulting from mountain topography, ownership boundaries, and microclimate gradients. In all these examples, the MODIS data alone are insufficient for decisionmaking, but the combination of spatial coverage and consistent continuous temporal monitoring provides valuable new insights into vegetation dynamics across landscapes.

Future availability of MODIS GPP and NPP

In the future, weekly mapping of terrestrial GPP and annual NPP should be as routine as the weather data that are presented today. Like weather maps, maps of GPP and NPP might even be shown occasionally on the evening news when abnormal conditions are discovered. To make these data easier for nonscientists to interpret, we present the daily GPP and annual NPP as anomalies (departures from normal) from the historical data in our 1982–2003 GPP/NPP database. We compute the 21-year average GPP for each pixel for each month and compare the most recent computed GPP to this long-term average (figure 11). This depiction of GPP, showing areas of recent above- or below-normal activity, is easily interpreted and mimics the way the public views weather information on the evening news report.

One goal of current MODIS research is to use the 8-day GPP to set the initializing conditions for an ecological forecast of future GPP. We now have prototypes of this type of biospheric prediction in a terrestrial observation and prediction system (*www.ntsg.umt.edu/tops/*). Among other possible uses, this forecasting could provide a tool for disease control. Hantavirus pulmonary syndrome is propagated by infected mice whose population cycles are highly correlated with the productivity of desert vegetation. Satellite monitoring of the changing length of vegetation growing seasons, and prediction of the seasonal timing of primary productivity, may provide health officers with an early warning system for disease outbreaks and colonization into new areas (Glass et al. 2000).

The National Polar Orbiting Environmental Satellite System (NPOESS) provides a long-range plan for the future heritage of AVHRR and MODIS sensors (Townshend and Justice 2002). NPOESS is planned for first deployment in 2009, after the planned retirement of current AVHRR sensors and the two MODIS sensors currently in orbit. NPOESS will continue to produce the data stream initiated by MODIS for GPP and NPP. At that point, we expect these weekly GPP and annual NPP data to be a routine part of land management, environmental policy analysis, agricultural economics, and monitoring of biospheric change. While we are optimistic about the general quality and reliability of these data, they do not meet all the needs and expectations of scientists, managers, policymakers, and the public. These satellite-derived data products however, are unique in that they provide global coverage and weekly continuity of a key measure of terrestrial ecosystem activity.

Acknowledgments

References cited

Baldocchi D, et al. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bulletin of the American Meteorological Society 82: 2415–2434.

Bonan GB, Levis S, Kergoat L, Oleson KW. 2002. Landscapes as patches of plant functional types: An integrating concept for climate and ecosystem models. Global Biogeochemical Cycles 16 (2): 1021 (doi: 10.1029/2000GB001360).

Burke IC, Kittel TGF, Lauenroth WK, Snook P, Yonker CM, Parton WJ. 1991. Regional analysis of the central Great Plains. BioScience 41: 685–692.

Churkina G, Running SW. 1998. Contrasting climatic controls on the estimated productivity of different biomes. Ecosystems 1: 206–215.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA. 2001. Net primary production in tropical forests: An evaluation and synthesis of existing field data. Ecological Applications 11: 371–384.

Dickinson RE. 1996. Land surface processes and climate modeling. Bulletin of the American Meteorological Society 76: 1445–1448.

Falge E, et al. 2002. Phase and amplitude of ecosystem carbon release and uptake potentials as derived from FLUXNET measurements. Agriculture and Forest Meteorology 113: 75–95.

Field CB, Randerson, JT, Malmstrom CM. 1995. Global net primary production: Combining ecology and remote sensing. Remote Sensing of Environment 51: 74–88.

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. Science 281: 237–240.

Glass GE, et al. 2000. Using remotely sensed data to identify areas at risk for hantavirus pulmonary syndrome. Emerging Infectious Diseases 6: 238–247.

Goward SN, Tucker CJ, Dye DG. 1985. North American vegetation patterns observed with the NOAA-7 AVHRR. Vegetatio 64: 3–14.

Haberl H, Geissler S. 2000. Cascade utilization of biomass: Strategies for a more efficient use of a scarce resource. Ecological Engineering 16: S111–S121.

Hicke JA, Asner GP, Randerson JT, Tucker CJ, Los S, Birdsey R, Jenkins JC, Field C. 2002. Trends in North American net primary productivity derived from satellite observations, 1982–1998. Global Biogeochemical Cycles 16 (2): 1018 (doi: 10.1029/2001GB001550).

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D, eds. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press.

Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83: 195–213.

Hunt ER Jr. 1994. Relationship between woody biomass and PAR conversion efficiency for estimating net primary production from NDVI. International Journal of Remote Sensing 15: 1725–1730.

Hunt ER, Everitt JR, Ritchie JH, Moran JC, Booth MS, Anderson DT, Clark GL, Seyfried MS. 2003. Applications and research using remote sensing for rangeland management. Photogrammetric Engineering and Remote Sensing 69: 675–693.

Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW. 2001. Water in a changing world. Issues in Ecology 9: 1–16.

Justice CO, Townshend JRG, Vermote EF, Masuoka E, Wolfe RE, Saleous N, Roy DP, Morisette JT. 2002. An overview of MODIS Land data

processing and product status. Remote Sensing of Environment 83: 3–15.

Kates RW, et al. 2001. Sustainability science. Science 292: 641–642.

Keane RE, Burgan R, Wagtendonk JV. 2001. Mapping wildland fuels for fire management across multiple scales: Integrating remote sensing, GIS and biophysical modeling. International Journal of Wildland Fire 10: 301–319.

Keeling CD, Bacastow RB, Bainbridge AE, Ekdahl CA Jr, Guenther PB, Waterman LS. 1976. Atmospheric carbon dioxide variations at Mauna Loa Observatory, Hawaii. Tellus 28: 538–551.

Knapp AK, Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291: 481–484.

Lieth H, Whittaker RH, eds. 1975. Primary Productivity of the Biosphere. New York: Springer-Verlag.

Monteith JL. 1972. Solar radiation and productivity in tropical ecosystems. Journal of Applied Ecology 9: 747–766.

Morisette JT, Privette JL, Justice CO. 2002. A framework for the validation of MODIS land products. Remote Sensing of Environment 83: 77–96.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386: 698–702.

Myneni RB, et al. 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sensing of Environment 83: 214–231.

[NASA] National Aeronautics and Space Administration. 1983. Land-Related Global Habitability Science Issues. Washington (DC): NASA. Technical Memorandum no. 85841.

Nemani R, White M, Thornton P, Nishida K, Reddy S, Jenkins J, Running S. 2002. Recent trends in hydrologic balance have enhanced the terrestrial carbon sink in the United States. Geophysical Research Letters 29 (10): 1468 (doi: 10.1029/2002GL014867).

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300: 1560–1563.

Nicholson SE, Tucker CJ. 1998. Desertification, drought, and surface vegetation: An example from the West African Sahel. Bulletin of the American Meteorological Society 79: 815–829.

Niemeijer D. 2002. Developing indicators for environmental policy: Data-driven and theory-driven approaches examined by example. Environmental Science and Policy 5: 91–103.

Potter CS. 1999. Terrestrial biomass and the effects of deforestation on the global carbon cycle. BioScience 49: 769–778.

Potter CS, Davidson E, Nepstad D, Carvalho CR. 2001. Ecosystem modeling and the dynamic effects of deforestation on trace gas fluxes in Amazon tropical forests. Forest Ecology and Management 152: 97–117.

Prince SD, Goward SN. 1995. Global primary production: A remote sensing approach. Journal of Biogeography 22: 815–835.

Randerson JT, Thompson MV, Conway TJ, Fung IY, Field CB. 1997. The contribution of terrestrial sources and sinks to trends in the seasonal cycle of atmospheric carbon dioxide. Global Biogeochemical Cycles 11: 535–560.

Reeves MR. 2004. Agricultural and rangeland productivity patterns in the northern Great Plains estimated with MODIS vegetation data. PhD dissertation, University of Montana, Missoula.

Running SW, Nemani RR. 1988. Relating seasonal patterns of the AVHRR vegetation index to simulated photosynthesis and transpiration of forests in different climates. Remote Sensing of Environment 24: 347–367.

Running SW, Nemani RR, Peterson DL, Band LE, Potts DF, Pierce LL, Spanner MA. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation. Ecology 70: 1090–1101.

Running SW, Baldocchi DD, Turner DP, Gower ST, Bakwin PS, Hibbard KA. 1999. A global terrestrial monitoring network integrating tower fluxes,

flask sampling, ecosystem modeling and EOS satellite data. Remote Sensing of Environment 70: 108–127.

Running SW, Thornton PE, Nemani RR, Glassy JM. 2000. Global terrestrial gross and net primary productivity from the earth observing system. Pages 44–57 in Sala O, Jackson R, Mooney H, eds. Methods in Ecosystem Science. New York: Springer-Verlag.

Sala OE, et al. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Schaefer K, Denning AS, Suits N, Kaduk J, Baker I, Los S, Prihodko L. 2002. Effect of climate on interannual variability of terrestrial CO_2 fluxes. Global Biogeochemical Cycles 16 (4): 1102 (doi: 10.1029/2002GB001928).

Schimel DS. 1995. Terrestrial biogeochemical cycles: Global estimates with remote sensing. Remote Sensing of Environment 51: 49–56.

———. 1999. The terrestrial biosphere and global change: Implications for natural and managed ecosystems. Nature 400: 522–523.

Schulze E-D, Kelliher FM, Körner C, Lloyd JN, Leuning R. 1994. Relationships among stomatal conductance, ecosystem surface conductance, carbon assimilation rates, and plant nitrogen nutrition: A global ecology scaling exercise. Annual Review of Ecology and Systematics 25: 629–660.

Scurlock JMO, Olson RJ. 2002. Terrestrial net primary productivity—a brief history and a new worldwide database. Environmental Reviews 10: 91–109.

Sellers PJ. 1987. Canopy reflectance, photosynthesis, and transpiration, pt. II: The role of biophysics in the linearity of their interdependence. Remote Sensing of Environment 21: 143–183.

Sellers PJ, Mintz Y, Sud YC, Dalcher A. 1986. A simple biosphere model for use with general circulation models. Journal of Atmospheric Science 43: 505–531.

Tans PP, Fung IY, Takahashi T. 1990. Observational constraints on the global atmospheric CO_2 budget. Science 247: 1431–1438.

Thornton PE, et al. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agricultural and Forest Meteorology 113: 185–222.

Townshend JRG, Justice CO. 2002. Towards operational monitoring of terrestrial systems by moderate resolution remote sensing. Remote Sensing of Environment 83: 351–359.

Tucker CJ, Townshend JRG, Goff TE. 1985. African landcover classification using satellite data. Science 227: 369–374.

Turner DP, Urbanski S, Bremer D, Wofsy SC, Meyers T, Gower ST, Gregory M. 2003a. A cross-biome comparison of daily 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. 2003b. 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.

Waring R, Running SW. 1998. Forest Ecosystems: Analysis at Multiple Scales. San Diego: Academic Press.

Waring RH, Coops NC, Ohmann JL, Sarr DA. 2002. Interpreting woody plant richness from seasonal ratios of photosynthesis. Ecology 83: 2964–2970.

White MA, Thornton PE, Running SW, Nemani RR. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls. Earth Interactions 4 (3): 1–85.

Zhan X, Sohlberg RA, Townshend JRG, DiMiceli C, Carroll ML, Eastman JC, Hansen MC, DeFries RS. 2002. Detection of land cover changes using MODIS 250 m data. Remote Sensing of Environment 83: 336–350.

Zheng D, Prince S, Wright R. 2003. Terrestrial net primary production estimates for 0.5° grid cells from field observations—a contribution to global biogeochemical modeling. Global Change Biology 9: 46–64.