Review Article

Modeling and Monitoring Terrestrial Primary Production in a Changing Global Environment: Toward a Multiscale Synthesis of Observation and Simulation

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There is a critical need to monitor and predict terrestrial primary production, the key indicator of ecosystem functioning, in a changing global environment. Here we provide a brief review of three major approaches to monitoring and predicting terrestrial primary production: (1) ground-based field measurements, (2) satellite-based observations, and (3) process-based ecosystem modelling. Much uncertainty exists in the multi-approach estimations of terrestrial gross primary production (GPP) and net primary production (NPP). To improve the capacity of model simulation and prediction, it is essential to evaluate ecosystem models against ground and satellite-based measurements and observations. As a case, we have shown the performance of the dynamic land ecosystem model (DLEM) at various scales from site to region to global. We also discuss how terrestrial primary production might respond to climate change and increasing atmospheric CO_2 and uncertainties associated with model and data. Further progress in monitoring and predicting terrestrial primary production requires a multiscale synthesis of observations and model simulations. In the Anthropocene era in which human activity has indeed changed the Earth's biosphere, therefore, it is essential to incorporate the socioeconomic component into terrestrial ecosystem models for accurately estimating and predicting terrestrial primary production in a changing global environment.

1. Introduction

Terrestrial net primary production (NPP) refers to the net amount of carbon captured by plants through photosynthesis per unit time over a given period and is a key component of energy and mass transformation in terrestrial ecosystems. NPP represents the net carbon retained by terrestrial ecosystems after assimilation through photosynthesis (gross primary production (GPP)) and losses due to autotrophic respiration [1]. NPP is of fundamental importance to humans because the largest portion of our food supply comes from terrestrial NPP [2]. Additionally, NPP is an important indicator of ecosystem health and services [3–5] and a critical

component of the global carbon cycle [6, 7] that provides linkage between terrestrial biota and the atmosphere [8]. Research into terrestrial GPP and NPP, especially at a regional and global scale, has attracted much attention [3, 4, 9–11]. This is because they measure the transfer of energy to the biosphere and terrestrial CO_2 assimilation and provide a basis for assessing the status of a wide range of ecological processes [12].

NPP is an important ecological variable for evaluating trends in biospheric behavior [13] and investigating the patterns of food, fiber, and wood production [4] across broad temporal and spatial scales. Accurate estimations of global

NPP can improve our understanding of the feedbacks among the atmosphere-vegetation-soil interface in the context of global change [14] and facilitate climate policy decisions. Previous studies based on inventory analysis, empirical and process models, and remote sensing approaches have estimated global NPP in the range of 39.9–80 PgC yr^{-1} [3, 15–17]. In a recent meta-analysis study, Ito [18] reported a global terrestrial NPP of 56.4 PgC yr^{-1}. However, there is large uncertainty ($\pm$8-9 PgC yr^{-1}) in the estimation of global terrestrial NPP in recent years (2000–2010) making it difficult to evaluate the transfer of energy and the status of ecological processes [18]. These uncertainties are associated with sensitivity analysis and bias introduced by gap filling of satellite data. In addition, remote-sensing algorithm does not accurately account for environmental stresses such as rooting depth especially in dry areas where plants use deep roots to access and sustain water availability [19].

At a global scale, multiple environmental factors including climate, topography, soils, plant and microbial characteristics, and anthropogenic and natural disturbances control the timing and magnitude of terrestrial NPP [20]; however, the relative contributions of these environmental factors toward global NPP varies over time and space. Globally, climate change including changes in temperature and precipitation had a relatively small-scale positive impact on NPP during the period 1982–1999 [13]. However, during the last decade (2000–2009), the effect of climate on global NPP has been a subject of debate. Zhao and Running [6] reported that warming-related increases in water stress and autotrophic respiration in the Southern Hemisphere resulted in an overall decline in global NPP, whereas Potter et al. [21] found an increasing trend in global NPP due to rapidly warming temperatures in the Northern Hemisphere during the period 2000–2009. While climatic variables such as solar radiation, temperature, and precipitation have been recognized as a key factor controlling the terrestrial NPP [6, 21], other environmental factors such as elevated CO_2, nitrogen deposition, and ozone exposure are also equally important in controlling the timing and magnitude of terrestrial NPP [22]. Additionally, natural and anthropogenic factors such as hurricanes, fires, logging, land cover and land use change, and insect damage also have a significant effect on terrestrial NPP [23–26]. Accurately quantifying the effect of different environmental drivers including climate on global terrestrial NPP requires an understanding of the controlling physiological and ecological processes that determine the timing and magnitude of terrestrial carbon uptake [27, 28].

Because there is substantial uncertainty in our knowledge of the environmental factors that control the magnitude of terrestrial NPP, continuous monitoring of global terrestrial NPP is critical for evaluating trends in biospheric behavior [13], investigating large-scale patterns in food and fiber production [4], and understanding the potential of terrestrial ecosystems for carbon sequestration from the atmosphere. Terrestrial NPP is identified as a primary monitoring variable by a number of studies [4, 29] and

interested organizations (the Environmental Sustainability Index; http://www.ciesin.columbia.edu/indicators/ESI/ and the National Research Council Report; http://www.nap.edu/bookds/0309068452/html/); however, continuous and consistent measurement of global terrestrial NPP that integrates ecosystem processes across broad temporal and spatial scales [30] has not been possible. Although regular monitoring of global terrestrial NPP has been feasible using imagery and the satellite-borne Moderate Resolution Imaging Spectroradiometer (MODIS) sensor, such approaches are limited by their coarse resolution and difficulty in converging with other high resolution datasets and process-based models [14, 31, 32].

Although several approaches have been used to monitor terrestrial primary production over the past two-decades ranging from site-level observations [33–35] to large-scale remote sensing [6, 13] and process-based modeling [3, 36–38], or a combination of site-level observations, remote sensing techniques, and/or process-based models [8, 9, 39], these approaches are associated with significant uncertainties where inconsistent estimates of terrestrial NPP are observed in response to global change [40–42]. A wide range of uncertainty comes from upscaling site- or stand-level primary production to a regional and global scale [14, 43], structural differences among models that are susceptible to forcing-data and parameter values constrained by observations [44, 45], and limitations in the parameterization of light use efficiency [31] and photosynthetically active radiation [31, 46]. Similarly, terrestrial primary production is not directly estimated from the remote sensing measurements but is modeled as a function of leaf area index and fraction of photosynthetic active radiation (fPAR) or greenness index. These indexes used to estimate terrestrial NPP are contaminated by atmospheric particles that would send misleading signals to satellite sensors [47]. Additionally, process-based models integrate the understanding of ecological and physiological processes obtained from field measurements and are particularly important to characterize the response of terrestrial ecosystems to different environmental stressor [23, 48]. It is, therefore, essential to integrate site-level, remote-sensing, and process-based modeling approach to accurately monitor and predict terrestrial primary production across broad temporal and spatial scales.

A variety of reviews have addressed various aspects of NPP [18, 49, 50]; however, none have comprehensively reviewed the existing approaches and associated uncertainties as well as future needs. Therefore, the purpose of this review is to (1) summarize the general approaches to estimate GPP and NPP at multiple scales; (2) review major environmental factors controlling the magnitude and timing of GPP and NPP; (3) identify uncertainties associated with large-scale GPP and NPP estimations; (4) recognize knowledge gaps with possible future direction under changing environmental conditions. Generally, three approaches have been used to estimate gross and net primary productivity in the terrestrial ecosystems: (1) ground-based monitoring including biomass inventory [35] and eddy covariance measurement [9]; (2) remote sensing-based observation [6]; (3) spatially explicit ecosystem modeling [51]. Here, we provide a brief

review of these approaches with an emphasis on satellite-based observation and terrestrial ecosystem modeling.

2. Ground-Based Monitoring of Terrestrial Primary Production

Ground-based monitoring of terrestrial primary production provides a basis for accurately estimating global NPP because it provides direct measurement of terrestrial primary production for scaling up from site to global level as well as calibrating and validating both satellite- and model-based approaches. Ground-based measurements of terrestrial primary production rely on two approaches: biomass and flux measurements. Since the International Biological Program (IBP, 1965–1974), a number of ecosystem surveys have been carried out to measure terrestrial primary production across the globe. Traditionally, terrestrial primary production estimation, using biomass measurement was carried out through periodic measurements of root, stem, leaf, and fruit growth. Recent technological advances allow for ground-based monitoring of terrestrial NPP using meteorological towers that measures the instantaneous exchange of CO_2 (net ecosystem exchange (NEE)) between the atmosphere and terrestrial ecosystems. Terrestrial NPP is calculated indirectly by adding heterotrophic respiration to NEE. Eddy covariance technique [52] is employed worldwide across different biomes including forest, cropland, grassland, and desert. Below, we provide a brief overview of two most widely used ground-based monitoring of terrestrial primary production: (a) biomass inventory and (b) flux measurements using eddy covariance technique.

2.1. Biomass Inventory. The biomass inventory data provide valuable sources of information for estimation of biomass and NPP in forest, cropland, and grassland at landscape and regional scales [53, 54]. Since the early 1980s, regional or national inventories, with a large number of statistically valid plots, have been widely regarded as a powerful tool for estimating forest and crop biomass at broad scales [55, 56]. Inventory-based method estimates forest biomass using biomass expansion factor (BEF) that converts stem volume to biomass to account for noncommercial components, that is, branches, root, and leaves, and so forth [57–59]; however, other studies have indicated that total stem volume varies with forest age, site class, and stand density [60–63]. An alternative approach to tree biomass estimation includes the allometric equation, which can be converted to CO_2 equivalents by scaling [64]. Estimates of forest biomass based on an allometric equation have been used widely to examine the impacts of forest management [65], land-use change [66], and increase in atmospheric CO_2 [67]. While allometric equations are important for estimating forest biomass and are used widely in growth and yield models (e.g., Forest Vegetation Simulator), they fail in distinguishing and quantifying the relative contribution of land cover and land-use change and several environmental factors including climate, elevated CO_2, and air pollution on carbon uptake. Recently, Houghton [68] has recognized that keeping land cover and land use change exclusive of the environmental change is critically important because it helps to separate direct anthropogenic effects from indirect or natural effects and lower the uncertainty of the land cover and land-use change flux.

2.2. Flux Measurements Using Eddy Covariance Technique. Eddy covariance technique estimates CO_2 exchange rate between atmosphere and plant canopy by measuring the covariance between fluctuation in vertical wind velocity and CO_2 mixing ratio [69, 70]. Eddy covariance technique made it possible to directly and continuously measure vertical turbulent fluxes within atmospheric boundary layers on short and long time scales (from 30 min to year). At the ecosystem scale, FLUXNET towers measure net ecosystem CO_2 exchange (NEE), which is equal to GPP minus ecosystem respiration [70] (i.e., the quantity of CO_2 respired by both autotrophs (plants) and heterotrophs (primarily microbes)). Since the 19 s, there has been increasing interest in estimating net CO_2 exchange in terrestrial ecosystems based on eddy covariance measurements [71]. The eddy covariance approach is capable of detecting small changes in net CO_2 exchange between terrestrial ecosystems and the atmosphere over various time scales [69]. The international FLUXNET [52] has established a network of FLUXNET towers on six of seven continents, including a number of regional networks of eddy covariance measurements (such as CarboeuropeIP, AmeriFlux, Fluxnet-Canada, LBA, AsiaFlux, ChinaFlux, CarboAfrica, KoFlux, TCOS-Siberia, and Afriflux). The flux data derived from these networks provide unprecedented detailed information to the broad community of scientists who need flux data to test, calibrate, validate, and improve land surface schemes in climate models, dynamic vegetation models, remote sensing algorithms, hydrological models, and process-based ecosystem models. Eddy flux measurement also provides a unique tool for understanding eco-physiological mechanisms and environmental controls of ecosystem carbon processes in the context of global change. However, for the large-scale estimation of terrestrial primary production, current eddy covariance measurement sites are still too few and unevenly distributed. The regional extrapolation of carbon-storage capacity from a single field site to the whole study area/region has been based on an assumption of homogeneity in ecosystem functioning across this region, which brings large uncertainties. For instance, Xiao et al. [9] found that the upscaled eddy covariance terrestrial primary production (GPP) for the conterminous US was 14% higher compared to MODIS. The net carbon exchange between the biosphere and the atmosphere at the regional scale, however, can be very different from the product of a site-specific rate of exchange and the area of the region because terrestrial ecosystems have differential responses due to vegetation type, disturbance history, soil, and climate variables that vary over space and time [72]. In addition to upscaling issues, complex topography and unstable atmospheric condition can substantially alter the carbon fluxes due to nighttime gravitational or drainage flows [73], resulting in differences in carbon fluxes in the range of 80–200% compared to measurements based on inventory approach [74].

3. Satellite-Based Monitoring of Terrestrial Primary Production

Ground-based measurements of terrestrial primary production are usually made at spatial scales in the range of less than one to a few hundred square meters making it difficult to estimate terrestrial primary production at a regional and global scale. Additionally, ground-based measurements of terrestrial NPP are constrained by topographic complexity and other adverse environmental factors. Satellite-based monitoring of terrestrial primary production is particularly important over large areas where ground-based methods (inventory and eddy covariance) are not feasible. Satellite-based estimations provide a repeated, consistent measurement of terrestrial primary production across broad temporal and spatial scales. Below we provide a brief overview of satellite-based monitoring of terrestrial primary production with a focus on NASA's Moderate-Resolution Imaging Spectroradiometer (MODIS).

Remote sensing based estimation of terrestrial primary production has advanced tremendously over the past few decades, and these datasets provide essential information associated with emissions of CO_2 into the atmosphere at regional, continental, and global scales. Because carbon fluxes (GPP and NPP) are difficult to measure over larger areas due to high spatial heterogeneity, satellite observations provide consistent, spatially fine-scale estimates [75] and allow us to monitor ecosystem patterns and activities at larger scales [6]. Since the pioneering work of Tucker et al. [76] on the correlation between remote sensing-derived vegetation index (i.e. the Normalized Difference Vegetation Index (NDVI)) and photosynthetic activity, satellite remote sensing has become a primary source of data on regional ecosystem patterns and terrestrial primary production. Additionally, satellite based observations have been coupled with mathematical models to quantify the carbon fluxes across the globe. For instance, over the last decades, production efficiency models (PEM) have been developed based on available satellite data, to monitor primary production and investigate the carbon cycle at large scales [31, 77]. One of the most promising tools to track changes in the productivity of terrestrial and marine ecosystem is based on GPP/NPP products derived from NASA's Moderate-Resolution Imaging Spectroradiometer (MODIS), a satellite-mounted instrument that collects surface spectral signatures to quantify the changes in terrestrial primary production over large areas. Below, we describe detail algorithms on how MODIS keeps track of changes in primary productivity over time to enhance our understanding on how satellite observations are used to estimate terrestrial productivity.

Detailed information on MOD17 algorithm is available in the MOD17 Algorithm Theoretical Basis Document (ATBD) [78] or MOD17 user's guide. Here we provide a simple overview of MOD17. The MOD17 algorithm can be mainly divided into two steps. First, we calculate daily GPP and MODIS photosynthesis product (PSNnet). The daily GPP is calculated as a function of conversion efficiency, incident short wave radiation, and fraction of photosynthetically

active radiation. PSNnet is obtained after subtracting maintenance respiration from the daily GPP. Second, we calculate annual NPP by summation of all 8-day PSNnet products after subtracting maintenance respiration of live wood and growth respiration of whole plant. Below, we provide a detailed description of the two steps.

The first step is calculation of daily GPP $(gC\,m^{-2}\,d^{-1})$ and PSNnet $(gC\,m^{-2}\,d^{-1})$, where PSNnet is equal to GPP minus maintenance respiration (MR) $(gC\,m^{-2}\,d^{-1})$ of leaves and fine roots, for each 8-day period. The standard global 8-day composite MOD17A2 products are formed by summation of these 8-day daily GPP and PSNnet with the first Julian day of the 8-day period as MOD17A2 time information in 10 degree HDF-EOS file name. Daily GPP is calculated similar to Heinsch et al [79] as follows:

$$GPP\varepsilon \times (SWrad \times 0.45) \times fPAR, \qquad (1)$$

where ε is the conversion efficiency (i.e., the amount of carbon a specific biome can produce per unit of energy) and SWrad $(MJ\,m^{-2}\,d^{-1})$ is the daily sum of incident solar short wave radiation, which is multiplied by 0.45 [80] to estimate fraction of photosynthetically active radiation (fPAR; $MJ\,m^{-2}\,d^{-1}$). SWrad is from the Data Assimilation Office (DAO) at NASA Goddard Space Flight Center (GSFC) and will be discussed in detail later. fPAR is from MOD15A2, 8-day composite fPAR, and LAI, which is based on the maximum fPAR value.

Daily ε $(gC\,MJ^{-1})$ is calculated from maximum ε under optimal conditions [79] when controlled by environmental stresses (lower temperature and drought) and is calculated as follows:

$$\varepsilon = \varepsilon_{max} \times f(T_{min}) \times f(VPD), \qquad (2)$$

where ε_{max} is the maximum biome-specific value under well-watered conditions, T_{min} is daily minimum temperature (°C), and VPD is daytime vapor pressure deficits (Pa). Linear interpolation functions of $f(T_{min})$ and $f(VPD)$ convert T_{min} and VPD to scalars ranging from 1 (optimal conditions) to 0 (extremely stressed conditions). Currently, ε_{max} is constant for a given biome. For different days, T_{min}, VPD, and SWrad are variable to weather conditions; hence, ε would be strongly related to different weather situations and GPP would change daily. For most ecosystems, the scalar of T_{min} controls photosynthesis during a relative short period at the beginning and end of the growing season. During most of the growing season, the scalar of T_{min} would be 1 due to higher T_{min} and would exert no constraint on assimilation so VPD and SWrad would be the two primary meteorological factors governing daily GPP in the MOD17 algorithm.

Maintenance respiration (MR, $gC\,m^{-2}\,d^{-1}$) by leaf and root is exponentially related to daily average temperature $(T_{avg},$ °C) as follows:

$$MR\_leaf = Leaf\_Mass \times leaf\_mr\_base \times Q_{10}^{[(T_{avg}-20)/10]}$$

$$MR\_root = Fine\_Root\_Mass \times froot\_mr\_base \times Q_{10}^{[(T_{avg}-20)/10]}, \qquad (3)$$

where Leaf_Mass is retrieved from MOD15A2 LAI using biome-specific specific leaf area (SLA). Fine_Root_Mass is estimated from biome-specific constant ratios between leaf and fine root. Q_{10} is a respiration quotient and is assigned to be 2.0 across biomes. Leaf_mr_base and froot_mr_base are the maintenance respiration of leaves and fine toots per unit mass at 20°C.

The second step is the calculation of annual NPP ($gC\,m^{-2}\,y^{-1}$) by summation of all 8-day composite PSNnet and subtraction of MR of living wood and growth respiration (GR, $gC\,m^{-2}\,y^{-1}$) of whole-plant as follows:

$$\begin{aligned} NPP = \sum PSNnet - Livewood\_MR - Leaf\_GR \\ - Froot\_GR - Livewood\_GR - Deadwood\_GR, \end{aligned} \tag{4}$$

where Livewood_MR and Livewood_GR are the maintenance respiration and growth respiration of living wood, respectively. Leaf_GR, Froot_GR, and Deadwood_GR are the growth respiration of leaves, fine roots, and dead wood, respectively.

The most significant assumption made in the MOD17 logic is that biome specific physiological parameters do not vary with space or time. These parameters are outlined in the Biome Properties Lookup Table (BPLUT). For each pixel, biome types are translated from MOD12Q1 Land Cover into MOD17 biomes. An initial evaluation of the MODIS 2001 GPP product was made by comparing MODIS GPP estimates with ground-based GPP estimates over $25\,km^2$ areas at a northern hardwoods forest site and a boreal forest site.

In addition to estimating NPP and vegetation patterns, remote sensing-based observations provide input data (i.e., land cover maps, leaf area index, fPAR, etc.) to set boundary conditions in the climate models, hydrological models, and process-based ecosystem models [81]. While a remote sensing based approach provides continuous and quantitative observations about ecosystem changes at large scale, they are subjected to large errors, if uncorrected. These errors come from atmospheric contamination of the remote sensing signal that interacts with ozone, water vapor, aerosols, and other atmospheric constituents [82]. Additionally, atmospheric haze and scattering from terrestrial surfaces can severely reduce data consistency [83]. There is a need to validate remote sensing based estimates of global primary production against ground measurements on a landscape and regional scale. On the other hand, remote sensing based estimates of terrestrial NPP do not isolate the relative contribution of different environmental and anthropogenic factors. Therefore, a better understanding of terrestrial primary production requires integrating process-based models with remote sensing approaches and validating the model output with field-based measurements (biomass inventory and eddy covariance measurement).

4. Process-Based Model Simulation and Prediction

Terrestrial ecosystem models provide a powerful tool to integrate our understanding on ecosystem processes and measurements/observations at multiple scales to investigate net primary production in response to multiple environmental factors in the complicated world [38, 51, 84]. Since the 1990s, there has been a dramatic increase in the use of terrestrial ecosystem models to estimate the NPP of terrestrial ecosystems at various spatial and temporal scales. Ecosystem modeling has evolved from empirical modeling that usually considers empirical correlation between ecosystem variables and climate elements (such as temperature, precipitation, and radiation) to process-based modeling, which is capable of investigating multiple responses of ecosystem processes to both environmental and anthropogenic factors at both regional [51, 84, 85] and global scales [3, 48, 86]. Process-based models play a central role in assessing and predicting the primary productivity and carbon cycle of the terrestrial biosphere in past, present, and future conditions [87]. Melillo et al. [3] provide the first NPP estimation using a process-based model (terrestrial ecosystem model (TEM)) at global scale, with an emphasis on responses of terrestrial NPP to climate and atmospheric CO_2 increase. Since then, an array of ecosystem models have been developed and applied to estimate NPP as influenced by multiple environmental factors, including climate, atmospheric CO_2, nitrogen availability, natural disturbances, air pollution, land use, and land cover change [84, 88, 89].

Modeling representation of photosynthesis and autotrophic respiration varies among terrestrial biosphere models. In process-based ecosystem models, a modified Farquhar model is usually used to simulate gross primary production. We take the dynamic land ecosystem model (DLEM, [51]) as an example to address how GPP and NPP are represented in modeling scheme. In DLEM, the canopy is divided into sunlit and shaded layers. GPP ($gC\,m^{-2}\,day^{-1}$) is calculated by scaling leaf assimilation rates ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$) up to the whole canopy:

$$\begin{aligned} GPP_{sun} &= 12.01 \times 10^{-6} \times A_{sun} \times Plai_{sun} \times day\,1 \times 3600 \\ GPP_{shade} &= 12.01 \times 10^{-6} \times A_{shade} \times Plai_{shade} \times day\,1 \times 3600 \\ GPP &= GPP_{sun} + GPP_{shade}, \end{aligned} \tag{5}$$

where GPP_{sun} and GPP_{shade} are gross primary productivity of sunlit and shaded canopy, respectively; A_{sun} and A_{shade} are assimilation rates of sunlit and shaded canopy; $Plai_{sun}$ and $Plai_{shade}$ are the sunlit and shaded leaf area indices; day l is daytime length (second) in a day. 12.01×10^{-6} is a constant to change the unit from $\mu mol\,CO_2$ to gram C.

The DLEM determines the C assimilation rate (A) as the minimum of three limiting rates, w_c, w_j, w_e, which are functions that represents the assimilation rates as limited by the efficiency of the photosynthetic enzymes system (Rubisco-limited), the amount of PAR captured by the leaf chlorophyll (light-limited), and the capacity of the leaf to export or utilize the products of photosynthesis (export-limited) for C_3 species, respectively. For C_4 species, w_e refer to the PEP carboxylase limited rate of carboxylation. The

canopy sunlit and shaded carbon assimilation rate can be estimated as

$$A = \min\left(w_c, w_j, w_e\right) \times \text{Index}_{gs}$$

$$w_c = \begin{cases} \dfrac{(c_i - \Gamma_*) V_{max}}{c_i + K_c \left(1 + o_i/K_o\right)} & \text{for } C_3 \text{ plants} \\ V_{max} & \text{for } C_4 \text{ plants} \end{cases}$$

$$w_j = \begin{cases} \dfrac{(c_i - \Gamma_*) \, 4.6\phi\alpha}{c_i + 2\Gamma_*} & \text{for } C_3 \text{ plants} \\ 4.6\phi\alpha & \text{for } C_4 \text{ plants} \end{cases} \tag{6}$$

$$w_e = \begin{cases} 0.5 V_{max} & \text{for } C_3 \text{ plants} \\ 4000 V_{max} \dfrac{c_i}{P_{atm}} & \text{for } C_4 \text{ plants,} \end{cases}$$

where c_i is the internal leaf CO_2 concentration (Pa); o_i is the O_2 concentration (Pa); Γ_* is the CO_2 compensation point (Pa); K_c and K_o are the Michaelis-Menten constants for CO_2 and O_2, respectively; α is the quantum efficiency; ø is the absorbed photosynthetically active radiation (W·M−2); V_{max} is the maximum rate of carboxylation which varies with temperature, foliage nitrogen concentration, and soil moisture:

$$V_{max} = V_{max\,25} a_{v\,max}^{(T_{day}-25)/10} f(N) f\left(T_{day}\right) \beta_t, \tag{7}$$

where $V_{max\,25}$ is the value at 25 and $a_{v\,max}$ is a temperature sensitivity parameter; $f(T_{day})$ is a function of temperature related metabolic processes; $f(N)$ is nitrogen scalar of photosynthesis which is related to foliage nitrogen content. β_t is a function, ranging from one to zero, which represents the soil moisture and lower temperature effects on stomatal resistance and photosynthesis.

The DLEM separates autotrophic respiration into maintenance respiration (Mr, unit: $gC\,m^{-2}\,day^{-1}$) and growth respiration (Gr, unit: $gC\,m^{-2}\,day^{-1}$). Gr is calculated by assuming that the fixed part of assimilated C will be used to construct new tissue (for turnover or plant growth). During these processes, 25% of assimilated C is supposed to be used as growth respiration. Maintenance respiration is related to surface temperature and biomass nitrogen content [51]. NPP is thus calculated as

$$Gr = 0.25 \times GPP$$
$$NPP = GPP - Mr - Gr. \tag{8}$$

Terrestrial ecosystem models are important tools for synthesizing a huge quantity of data, analyzing and predicting large-scale ecosystem processes, and providing a dynamic constraint on uncertainties in a variety of issues related to complex ecosystem processes, as well as heuristics clue for empirical studies [90–92]. This process-based modelling approach avoids many of the limitations of forest biomass inventories, eddy covariance measurement, and inverse modelling by accounting for ecosystem processes and spatial variations in environmental factors. Theoretically, the use of the spatially explicit ecosystem modelling approach provides

us with the ability to determine the relative roles of climate, CO_2, land use and land cover change, air pollution, and disturbances to changes in terrestrial primary production and other carbon fluxes. However, this approach also has its own limitations because of the uncertainties associated with estimates of key model parameters as well as an incomplete understanding of ecosystem processes [84, 93]. The accuracy of process-based modeling on estimation of terrestrial primary production depends on comparison of simulated NPP across broad temporal and spatial scales with observations at a stand or landscape level (biomass inventory and eddy covariance techniques) and with satellite based estimates at a regional and global level.

5. Evaluating Process-Based Ecosystem Model against Ground and Satellite Observations

Model validation is essential for establishing the credibility of ecosystem models. Rastetter [92] divided various approaches for validating a biogeochemical model into four categories: (1) tests against short-term data; (2) space-for-time substitutions; (3) reconstruction of the past; (4) comparison with other models. To evaluate the accuracy of simulated terrestrial primary production, modeled GPP or NPP has been validated against experimental and observational data from field measurements and biomass inventory and also evaluated against satellite-based estimates and though model intercomparison. Here we use the DLEM model as a case for demonstrating how we validate and evaluate ecosystem models.

5.1. Evaluating against Flux Measurement Data. The DLEM-simulated GPP was compared with the observational data from the AmeriFlux towers in the Southeastern United States. These sites include Duke Forest Hardwoods, Duke Forest Loblolly Pine, Shidler Tallgrass Prairie site, and ARM-Southern Great Plains (SGP) site. We extracted GPP from our regional simulation (8 km × 8 km resolution) for the specific sites and compared that with eddy covariance estimates. Our results show that DLEM-simulated GPP is in a good agreement with eddy covariance based GPP for both forests and grassland sites (Figures 1(a)–1(d)). Generally, the model results fit well with observed GPP at Duke Hardwoods, Duke Loblolly, and Shidler Tallgrass except ARM-Southern Great Plain site. The ARM-Southern Great Plain site is a cropland site where measurements were available for limited time period when the vegetation is not in the most active growth period resulting in poor performance of model prediction.

5.2. Evaluating against Stand and Regional Biomass Inventory Data. The DLEM-simulated NPP was also compared to the site observation data in the Southern United States (SUS). We selected 138 measurements from the multibiome forest NPP dataset published by the Oak Ridge National Laboratory (ORNL) Distributed Active Archive Center. We extracted simulated NPP from our regional simulation outputs (8 km × 8 km per pixel) to match the geographic information of these

(a)

(b)

(c)

(d)
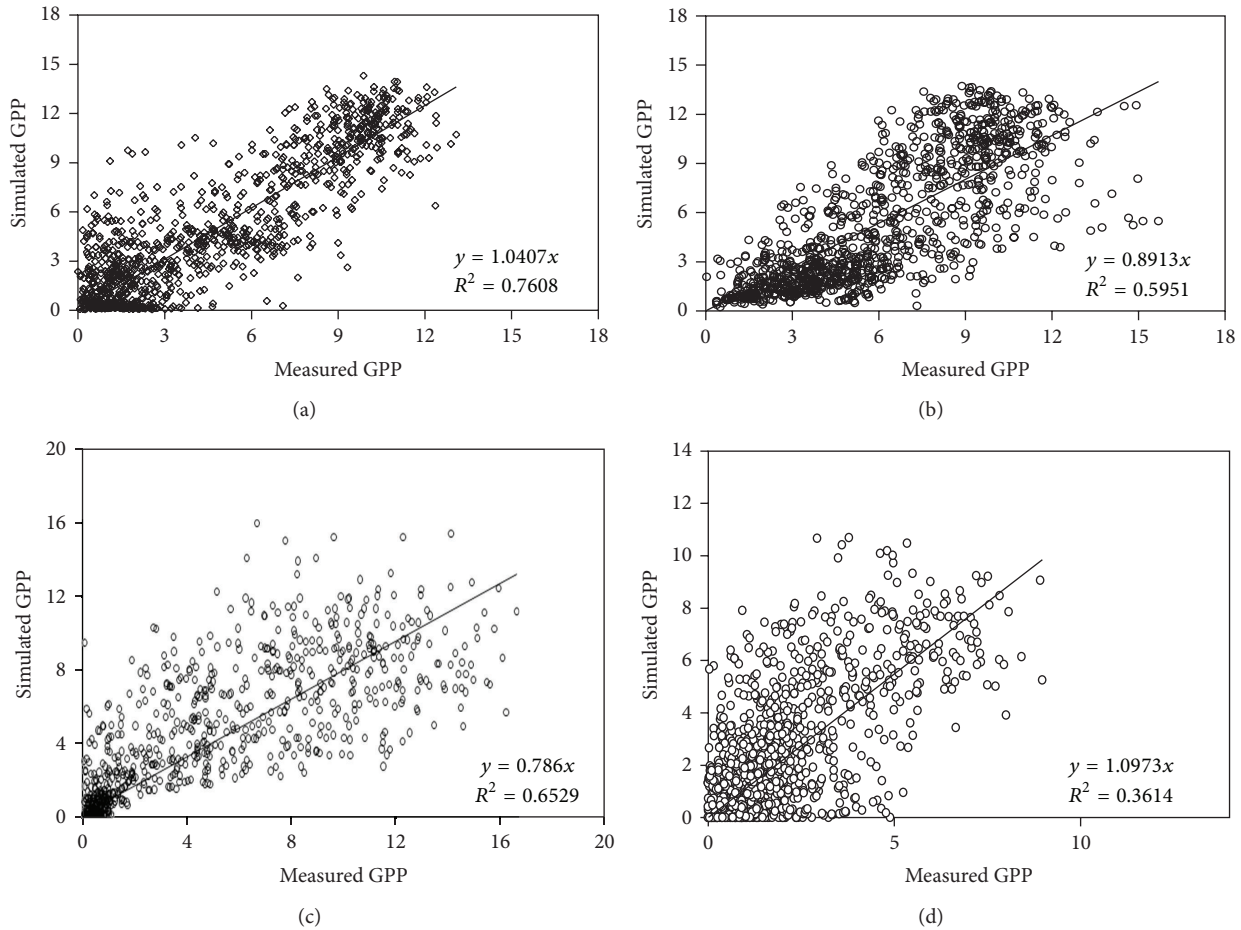
Figure 1: Evaluation of DLEM-simulated GPP against eddy covariance measured daily GPP (gC/m^2/day) at sites: (a) Duke Forest Hardwoods (US-DK2, NC, USA, deciduous broadleaf forest) from 2003 to 2005; (b) Duke Forest Loblolly Pine (US-DK3, evergreen needleleaf forest) from 2003 to 2005; (c) Shidler Tallgrass Prairie (US-shd, OK, USA, C4 grassland) from 1998 to 1999; (d) ARM SGP Main (US-arm, OK, USA, cropland) from 2003 to 2006.

138 sites. There was a good agreement between the simulated and measured aboveground NPP (Figure 2(a), slope = 1.09, and R^2 = 0.82).

For the purpose of regional validation, we compared DLEM simulated crop NPP with survey reports based on Huang et al. [94] at a national level across China. Our DLEM simulated NPP matched well with Huang et al.'s [94] observed NPP collected across 30 provinces in China (Figure 2(b), slope = 0.96, R^2 = 0.73). Additionally, we compared the model simulated state-level vegetation carbon of the southern ecosystem against the reported value based on forest inventory dataset (http://www.fia.fs.fed.us/). The comparisons (Figure 2(c)) showed that the vegetation carbon simulated by DLEM matched well with the results derived from the forest inventory database for year 1987 and 1997.

5.3. Evaluating against Satellite-Based Estimates. We evaluated the temporal pattern of crop NPP in China during the period 1982–2005 against the remote sensing dataset (Figure 3). We particularly compared our simulated crop

NPP with results from the Global Production Efficiency Model (GLO-PEM), which has a spatial resolution of 8 km and runs at a 10-day time step. GLO-PEM was driven almost entirely by satellite-derived variables, including both the Normalized Difference Vegetation Index (NDVI) and meteorological variables [77, 95]. We overlaid the GLO-PEM NPP images with the yearly cropland distribution data that we had developed and extracted previously. Similarly, we obtained the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD 17 NPP from 2002 to 2005 and the Advanced Very High Resolution Radiometer (AVHRR) NPP from 1981 to 2001 [4]. The results showed that the DLEM-simulated NPP had the same temporal pattern with relatively higher values than those provided by GLO-PEM and by MODIS MOD 17. A possible explanation for the underestimation by GLO-PEM might be due to the fact that nitrogen is not factored into the model. MODIS MOD 17 results might be influenced by the LAI, which tends to be underestimated by MODIS MOD 17 [96]. Similarly, the uncertainties of input data and parameters adopted in DLEM
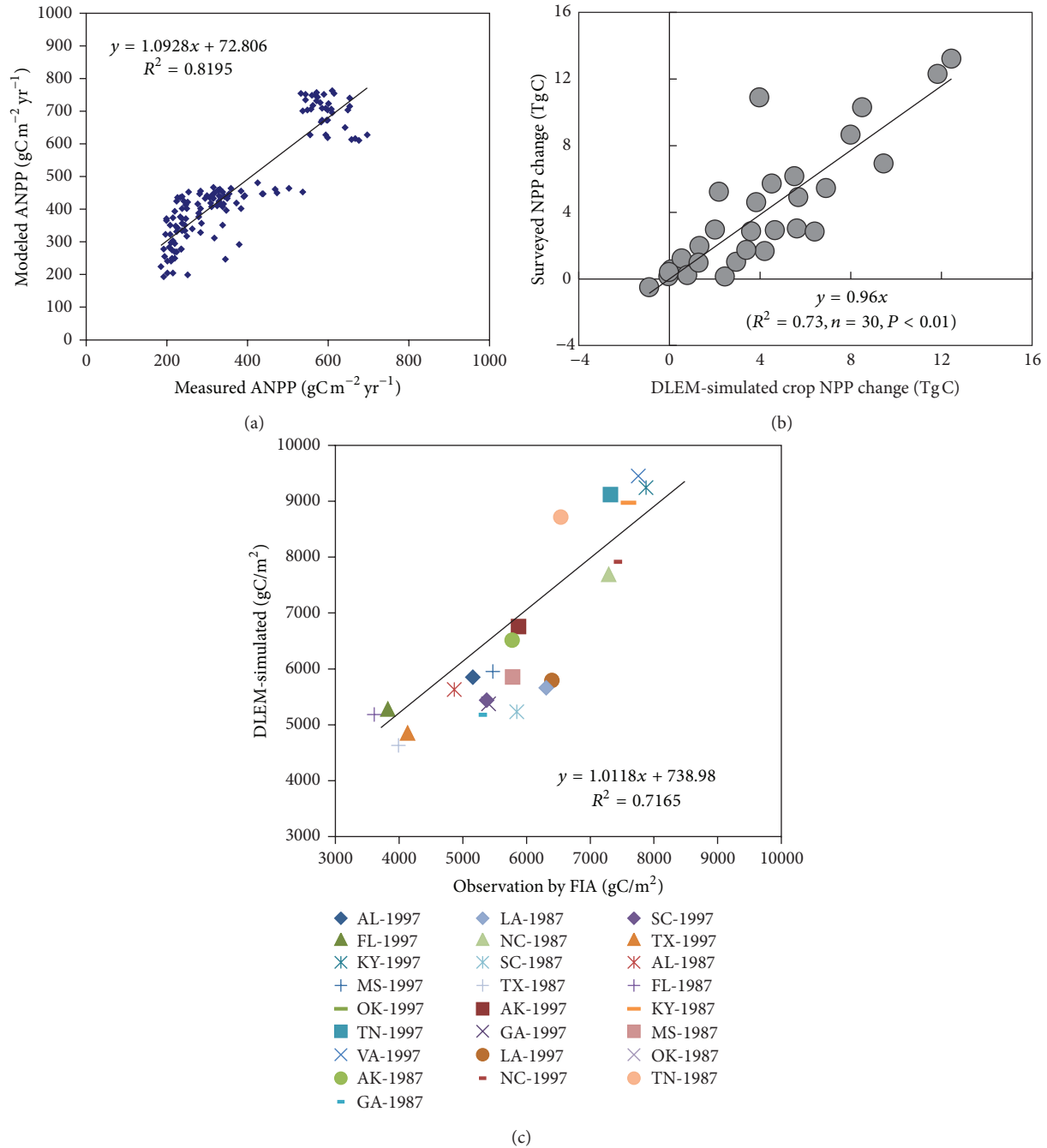
(a)

(b)

(c)

FIGURE 2: Comparisons of (a) modeled annual aboveground NPP against 138 field measurements in the SUS selected from Zheng et al. [120]; (b) modeled annual NPP against survey based crop NPP between 1980's and 1990's from Huang et al. [94]; (c) modeled vegetation carbon against forest inventory outputs in 1987 and 1997 based from Birdsey and Lewis [130].

could lead to higher simulated NPP; for example, we did not include vegetable crop types in this study and assumed that all croplands were dominant by cereal crop types.

We further evaluated DLEM's performance in simulating the spatial pattern of global GPP and NPP across the terrestrial biosphere by comparing it with MODIS product. The spatial pattern of the modeled GPP and NPP is consistent with that of MODIS GPP and NPP (Figure 4). However, the algorithms of MODIS for estimating NPP are not well

calibrated for cropland. A comparison of NPP measured at eddy covariance flux towers in China's cropland with MODIS-estimated NPP [97] indicated that MODIS has significantly underestimated the cropland NPP, which partly explained the higher estimates from the DLEM relative to MODIS products.

Finally, as a surrogate for the direct validation, model intercomparisons can be used to check the applicability of various kinds of ecosystem models [88]. Ecosystem models
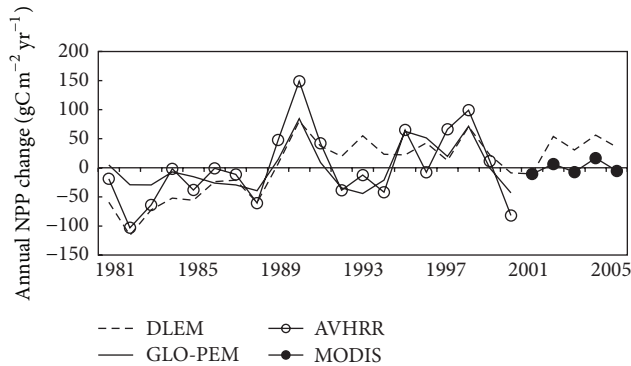
FIGURE 3: Temporal change in annual net primary production (NPP) (relative to the average for 1981–2005) of China's croplands estimated by DLEM-Ag model, GLO-PEM model, AVHRR, and MODIS database during 1981–2005) (modified from Ren et al. [131]).

differ among each other in terms of different model structure, parameters, and the processes that control photosynthetic carbon uptake. The estimates of terrestrial primary production among models, therefore, depend on inherent assumptions and complexity of model structure and formulation. For instance, previous model intercomparison studies [88, 89, 98] report large uncertainty associated with representation of vegetation structure, soil moisture dynamics, and ecosystem response to drought or humidity stress resulting in substantial differences in terrestrial primary production among the models. Although these models differ in assumptions, structure, parameters, and process representation, their intercomparison can highlight model weaknesses, inconsistencies, and uncertainties, which could provide insights for further model improvements. In addition, their intercomparison forces us to examine the interaction among data, model structure, parameter sets, and predictive uncertainty.

6. Assessing Terrestrial Primary Production Response to Climate Change and Increasing Atmospheric CO_2

Previous research has emphasized on how global change factors affect terrestrial primary production across broad temporal and spatial scales. Observational evidence suggest that earth's surface temperature has increased by 0.76°C over the past 150 years and is expected to increase by 1.5–6.4°C by the end of 21st century [99]. Historically, precipitation varied among regions over the period 1900–2005 but is expected to increase by 0.5–1% per decade in the 21st century at a global level [99]. These climate change factors would have a significant effect on ecosystem structure and function resulting in growing season extension [100], carbon loss [101], and changes in water balance [102]. Additionally, studies suggest that elevated CO_2 contributes to an enhancement in terrestrial primary production [67, 103, 104]; however, such enhancement may be counterbalanced by negative effects of ozone [105, 106]. Although tropospheric ozone has been considered as an important environmental factor that

controls terrestrial net primary production, its effect varies depending on regions [105, 106] and therefore could be less important compared to other environmental factors at a global scale. Another factor that might contribute to changes in terrestrial primary production is anthropogenic nitrogen inputs. Nitrogen enrichment has been primarily thought to stimulate terrestrial primary production in the temperate forest [107]; however, excessive nitrogen input likely leads to soil acidification, nutrient cation leaching, thus limiting plant growth [108]. Therefore, in this review, we only considered the effect of climate change and elevated CO_2 because they are the major factors affecting terrestrial primary production at a global scale [6, 13, 21].

6.1. Climate Change Impact on Terrestrial Primary Production. Climate factors (i.e., temperature, precipitation, and radiation) are key drivers to control changes in terrestrial primary production [38]. Plants assimilate carbon for growth through photosynthesis, which is strongly affected by temperature. Plants also need nutrients from the soil (i.e., nitrogen and phosphorus), and plant responses to climate change can be substantially modified by the nutrient availability. Nutrient availability itself can also be affected by climate factors, especially temperature, because the rate of soil nutrient mineralization strongly depends on temperature. Below the optimum temperature, the activity of photosynthesis increases with increasing temperature in accordance with the Arrhenius relationship [109]. At higher temperature, photosynthesis decreases due to conformational changes in key enzymes. This decrease is reversible at moderately high temperatures but becomes increasingly irreversible with increased duration and intensity of high temperature exposure [110]. Many previous studies suggest that global warming resulted in an increase in NPP [13, 111] during the period 1982–1999, especially in northern high latitude ecosystems. In the low latitude region, changes in long-term NPP patterns were mainly controlled by colimitations of sunlight and precipitation.

The temporal and spatial patterns of precipitation are also critical to terrestrial ecosystem processes [38]. Tao et al. [112] indicate that the precipitation was the key factor determining the spatial distribution and temporal trends of NPP in China during 1981–2000. Zhao and Running [6] suggest a reduction in the global NPP of 0.55 Pg C due to large-scale droughts, especially in the Southern Hemisphere, where decreased NPP counteracted the increased NPP over the Northern Hemisphere. However, Potter et al. [21] found an increasing trend in global NPP due to rapid warming trend that alleviated heat limitations in high latitude ecosystems in the Northern Hemisphere during the period 2000–2009. Additionally, comparison of 14 ecosystem models suggested that water availability is the primary limiting factor for NPP in global terrestrial ecosystem models [113].

While Intergovernmental Panel on Climate Change (IPCC, 2007) reported that the earth temperature is projected to increase during the 21st century that could largely alter ecosystem structure and function, it is still unclear how terrestrial primary production would respond to future climate change. Song et al. [114], using a dynamic land
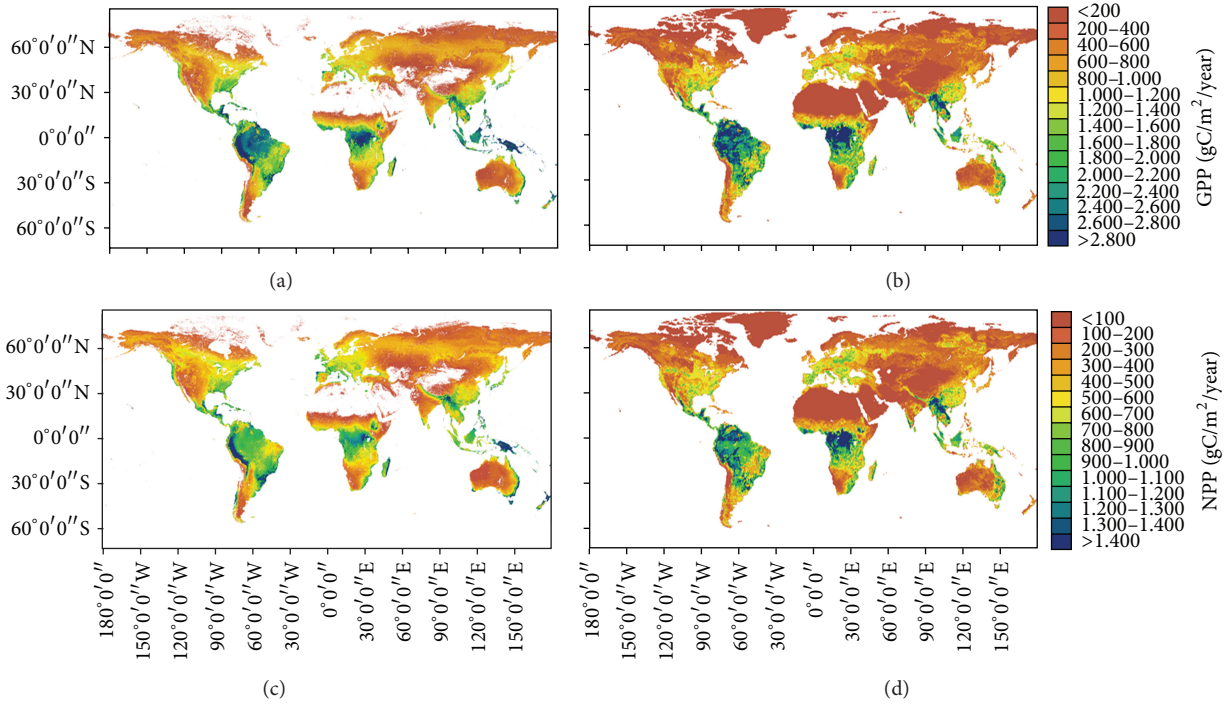
FIGURE 4: Spatial patterns of MODIS-derived and DLEM-simulated GPP and NPP for year 2010. MODIS-derived GPP (a) and NPP (c) and DLEM-simulated GPP (b) and NPP (d).
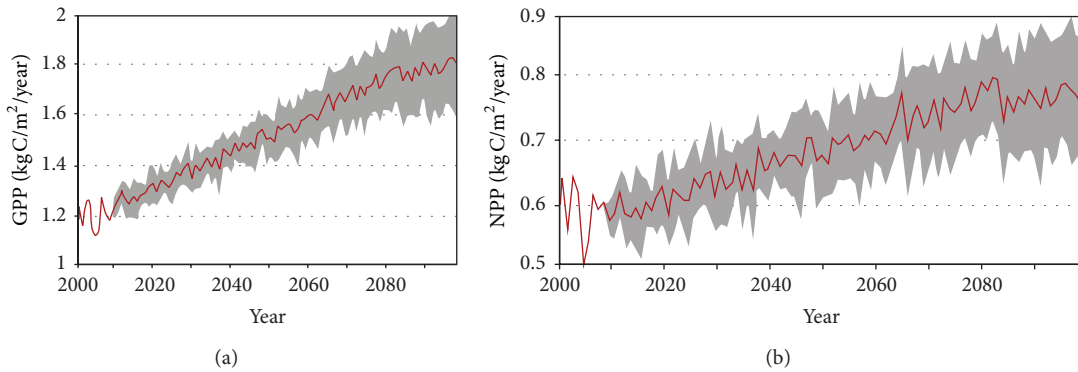

FIGURE 5: Projection of terrestrial primary production in response to climate change and increasing atmospheric CO_2 from 2000 to the 2090 as simulated by DLEM (a) change in gross primary production and (b) change in net primary production (modified from Song et al. [114]).

ecosystem model, projected an increase in GPP and NPP by 0.6 KgC m−2 yr^{-1} and 0.2 KgC m^{-2} yr^{-1}, respectively, during the period 2000–2099 (Figure 5) across the Southeastern US. Across the globe, Sitch et al. [115] projected global NPP under four SRES scenarios (A1FI, A2, B1, and B2) using five dynamic global vegetation models (DGVMs) and found reduction in terrestrial NPP due to climate. While five models show divergence in their response to climate, all models resulted in decrease in NPP in the tropics and extratropics. These results indicate that the estimated effect of climate on terrestrial NPP varies depending on emission scenarios and model structure and parameters used to simulate plant physiological response to global change.

While inventory and satellite based approaches provide estimates of terrestrial primary production at a global scale, these approaches do not allow us to separate the effects of climate and elevated CO_2. For instance, Zhao and Running [6] found that extreme events such as drought in the Southern Hemisphere resulted in a decline in terrestrial NPP, while Potter et al. [21] report an increase in NPP during the period 2000–2009. However, these studies do not necessarily specify whether such decline is due to specific climate factors or a combination of climate and elevated CO_2 or other environmental drivers. At a global scale, climate in the absence of elevated CO_2 reduced terrestrial NPP, while doubling CO_2 concentration under changing climatic condition increased global NPP by 25% [37].

TABLE 1: Published values of global terrestrial GPP and NPP based on observations, satellites, and/or process-based model.

Source	Basis	GPP (PgC yr^{-1})	NPP (PgC yr^{-1})
Melillo et al. [3]	TEM model	NA	53.2
Field et al. [20]	CASA model	NA	48.0
Schlesinger [126]	Review	NA	51.97
Cao and Woodward [37]	CEVSA model	NA	57.0
Ruimy et al. [50]	Model intercomparison	NA	45.5
Cramer et al. [15]	Model intercomparison	113	55.4 (44.4~66.3)
Zhao et al.[127]	MODIS	109.29	56.02
Beer et al. [8]	Diagnostic models	123 ± 8	NA
Yuan et al. [46]	Ameriflux and MODIS	110.5	NA
Ryu et al. [128]	MODIS and process-based model	118 ± 26	NA
Jung et al. [129]	Machine learning approach	119.4 ± 5.9	NA
Ito [18]	Meta-analysis	NA	56.2 ± 14.3
Potter et al. [21]	MODIS and CASA model	NA	50.05
This study	DLEM model	110.4	54.6

6.2. CO_2 Impact on Terrestrial Primary Production. The primary responses of plants to elevated atmospheric CO_2 concentration are increased photosynthesis and reduced stomatal conductance [116]. Stomata play an essential role in the regulation of both water losses by transpiration and CO_2 uptake for photosynthesis and plant growth. In order to optimize CO_2 uptake and water losses in rapidly changing environmental conditions, plants have evolved the ability to control stomatal conductance in response to multiple environmental factors such as solar radiation, temperature, VPD, and wind speed. Mechanistic scheme has been developed by Farquhar et al. [109] to describe leaf-level photosynthesis response to CO_2. Ball [117] developed the Ball-Berry empirical model to describe the behavior of stomatal conductance to water vapor as a function of environmental conditions and net photosynthetic rate. These two schemes have been widely used in existing process-based models to describe plant responses to CO_2 increase.

Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) analyzed the responses of NPP to doubled CO_2 from 355 to 710 ppmv among three biogeochemistry models and found that, for the conterminous United States, doubled atmospheric CO_2 causes NPP to increase by 5–11% [10]. King et al. [118] used a georeferenced model of ecosystem dynamics to explore the sensitivity of global carbon storage to changes in atmospheric CO_2 and climate; the results suggest that a doubling of atmospheric CO_2 from 280 ppm to 560 ppm enhances equilibrium global NPP by 16.9%. In a similar model intercomparison study using five dynamic global vegetation models (DGVMs), Sitch et al. [115] found that interaction of climate and atmospheric CO_2 increased terrestrial NPP for four different SRES scenarios over the 21st century.

We also compared DLEM-simulated NPP and GPP with previous studies (Table 1) based on observation, remote sensing, and other process-based models. DLEM simulated a global GPP of 116 PgC yr^{-1} for year 2010 which is within the range of 109–119 PgC yr^{-1} based on previous studies. For the same year, DLEM simulated a global NPP of 56.5 PgC yr^{-1} compared to the range of 44–66 PgC yr^{-1} estimated by previous studies. While most of the previous studies (Table 1) are based on different approaches, they have their own limitations in terms of field measurements, accuracy associated with satellite estimates, and accuracy of the ecosystem models. For instance, satellite measurements are sensitive to changes in atmospheric chemistry. Similarly, ecosystem models lack structural complexity to capture belowground processes [119]. Therefore, it is necessary to integrate field observations, satellite based approach, and ecosystem models to accurately quantify the terrestrial primary production across broad temporal and spatial scales.

6.3. Uncertainty in Estimating Terrestrial Primary Production. Multiple approaches for estimating and predicting terrestrial primary production lead to diversified conclusions (Table 1). Uncertainty in the estimations of terrestrial primary productivity may arise from input datasets (climate, land use, etc.,) and inventory datasets (for model calibration and validation) as well as from the model structure itself. The analysis of the seventeen models shows that global NPP ranged from 39.9 to 80.5 Pg C [40]. Many factors such as model structure, parameters, input data, and scaling may be responsible for such large uncertainty. One major source of uncertainty is the available inventory NPP datasets for model parameterization, calibration, and validation [120]. The NPP is measured at plot or field scales that may not represent the NPP at the

0.5° by 0.5° grid cell that is commonly used by global scale models. Therefore, direct intercomparison between field data obtained in different studies or comparison of these results with coarse resolution models can be misleading. In a model intercomparison for which all models reported results at 0.5° by 0.5° grid size, there was no suitable and consistent field NPP available since most measurements are conducted in the small areas ranging from <1 to several ha [15]. The second problem with available inventory datasets is the belowground biomass measurement. The belowground biomass is often not measured but is instead estimated using standard formulas. This may provide misleading results. Lauenroth et al. [121] have reported that amount of uncertainty associated with estimates of NPP was significantly influenced by the variability in the input data. For example, due to greater variability in the field measured belowground data than aboveground data, estimates of belowground NPP tended to have more uncertainty than estimates of aboveground NPP. Therefore, lack of available input dataset provides a significant uncertainty in models that estimate NPP at global scale using coarse resolution grid size.

In addition to the inventory NPP datasets for model calibration and validation, the input datasets such as land use and climate are other sources of uncertainty in most of the models. At the global scale, the impacts may be very small for land use as compared to climate or meteorological datasets [122]. Jung et al. [122] estimated GPP using different land cover maps, spatial land cover resolutions, meteorological data sets, and process-based terrestrial ecosystem models. Their results indicate a clear hierarchy of effects: a small effect of using different land cover maps, a somewhat higher but still relatively small effect of the spatial land cover resolution, a substantial effect due to changing the meteorological forcing, and the largest effect caused by using different models. In this way, model structure provides the largest uncertainty in the terrestrial primary productivity.

In the models, uncertainty in the estimation of NPP arises from different representations of ecological processes by different models. Because the components of terrestrial ecosystems and the interactions among them are complicated or not well understood, simplifying assumptions must be made to describe them in numerical models. Different modeling strategies may adopt different simplifying assumptions, leading to different model complexity and behavior. The uncertainties in the models are very large, both in terms of parameter-based and model structure related uncertainty. Models may range from the simple, empirically derived, correlation of net primary productivity with air temperature and precipitation (e.g., [123]) to the detailed models with detailed biochemistry (e.g. DLEM, LPJ, CLM).

Recent studies indicated that major uncertainties in simulating interannual variations of gross carbon uptake are strongly linked to the way of how and if biogeochemical cycles (carbon, water, and nitrogen) interact within the models which controls their sensitivity to meteorological conditions [122]. The observed relationships between forest GPP and mean annual temperature are strongly related to a corresponding gradient of nitrogen availability [124]. Therefore, accurate model representation of interactions among carbon, nitrogen, and water cycles is the key to reduce uncertainty in simulating terrestrial primary production [51, 125].

7. Toward a Multiscale Synthesis of Observations and Model Simulations

For the NPP estimation at large scales, none of the approaches mentioned above could solely fill in the gap of our understanding. Experiments and observations are always conducted at a specific scale. Multiscale experiments and observations provide data but are not capable of quantifying underlying mechanisms of changes in terrestrial primary production as influenced by multiple environmental factors. At the same time, modeling studies have been developing by integrating better understanding and more representations of biotic and abiotic processes. In order to provide diagnosis, quantification, and attribution of multiscale terrestrial primary production across the globe, it is critically needed to synthesize the various observation data and the modeled output at diverse spatial scales ranging from site to region to globe and temporal steps ranging from day to decade. More specifically, (1) a common driving database needs to be developed to characterize the environmental changes and to drive the model runs. The database includes time series of site-specific and gridded climate, atmospheric composition, land-cover/land-use change, and land management practices and auxiliary dataset on elevation, slope, aspect, vegetation cover types, soil properties, and so on. (2) The magnitude, spatial, and temporal patterns of terrestrial primary production need to be quantified by various approaches and datasets, including site-specific flux measurements, regional inventories, MODIS-derived GPP/NPP, and model simulations in a multimodel fashion. (3) Based on model evaluation and intercomparison, multiple model simulation experiments need to be conducted to distinguish the relative contributions of controlling processes and to identify their changes over space and time. Multiscale synthesis efforts need to provide useful information to reflect the status of terrestrial primary production, which could show further feedback to climate system, as well as to improve our understanding of the mechanisms responsible for terrestrial primary production. (4) Multiple approaches lead to diversified conclusions in terms of quantification and attribution of terrestrial primary production. Therefore, assessments of uncertainty will be an integral part of any synthesis project. In particular, uncertainties associated with each input driving dataset, model structure, parameters, scaling, and measurement need to be addressed. We expect that such a multiscale synthesis will provide a systematic assessment on terrestrial primary production and its driving forces at varied spatial scales.

Moreover, we are living in the new world of the Anthropocene in which human activity has indeed changed the earth's biosphere [132, 133]. Human activity such as land use change has been a primary factor affecting magnitude, spatial, and temporal patterns of terrestrial primary production across the globe. From both scientific and policy perspectives,

therefore, it is essential to incorporate socioeconomic component into terrestrial ecosystem models for better estimating and predicting terrestrial primary production in a changing global environment.

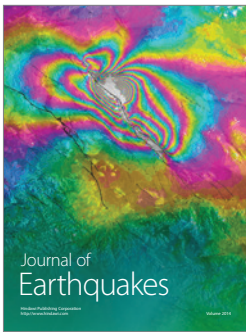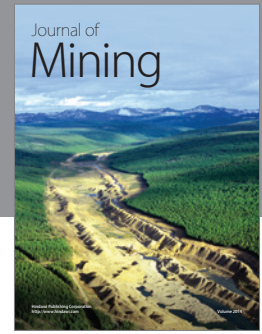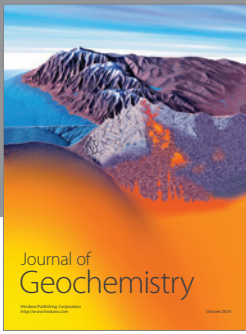## Conflict of Interests

Acknowledgments

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