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A historical meta-analysis of global terrestrial net primary productivity: are estimates converging?

AKIHIKO ITO*, †

*Center for Global Environmental Research, National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan, †Japan Agency for Marine-Earth Science and Technology, Yokohama, Kanagawa 236-0001, Japan

Abstract

Net primary productivity (NPP) is one of the most important ecosystem parameters, representing vegetation activity, biogeochemical cycling, and ecosystem services. To assess how well the scientific community understands the biospheric function, a historical meta-analysis was conducted. By surveying the literature from 1862 to 2011, I extracted 251 estimates of total terrestrial NPP at the present time (NPP_T) and calculated their statistical metrics. For all the data, the mean ± standard deviation and median were 56.2 ± 14.3 and 56.4 Pg C yr^{-1}, respectively. Even for estimates published after 2000, a substantial level of uncertainty (coefficient of variation by ± 15%) was inevitable. The estimates were categorized on the basis of methodology (i.e., inventory analysis, empirical model, biogeochemical model, dynamic global vegetation model, and remote sensing) to examine the consistency among the statistical metrics of each category. Chronological analysis revealed that the present NPP_T estimates were directed by extensive field surveys in the 1960s and 1970s (e.g., the International Biological Programme). A wide range of uncertainty remains in modern estimates based on advanced biogeochemical and dynamic vegetation models and remote-sensing techniques. Several critical factors accounting for the estimation uncertainty are discussed. Ancillary analyses were performed to derive additional ecological and human-related parameters related to NPP. For example, interannual variability, carbon-use efficiency (a ratio of NPP to gross photosynthesis), human appropriation, and preindustrial NPP_T were assessed. Finally, I discuss the importance of improving NPP_T estimates in the context of current global change studies and integrated carbon cycle research.

Keywords: carbon cycle, global change, meta-analysis, terrestrial biosphere, uncertainty

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Introduction

Net primary productivity (NPP), the carbon and energy fixed by green plants after their respiratory requirements have been met, is a key parameter of the biosphere that affects plant growth, biogeochemical cycling, biodiversity, carrying capacity of heterotrophic organisms, ecosystem resilience, and provisional services (e.g., foods and fibers). In the global carbon cycle, terrestrial NPP is one of the major flows, and many terrestrial human activities such as agriculture and forestry rely on NPP.

Ecologically, NPP is defined as the production of new dry-matter by primary producers during a certain period (Woodwell & Whittaker, 1968; Clark *et al*., 2001; Gower, 2002; Chapin *et al*., 2006), and it is available not only to producers (e.g., for growth, reproduction, and secondary metabolites) but also for consumers through foraging and following food web. NPP is calculated as follows:

$$\mathrm{NPP} = \Delta W + \mathrm{LF} + \mathrm{HB} + \text{residual consumption}, \quad (1)$$

where ΔW is the net increment of plant biomass including aboveground and belowground components, LF is abandonment of dead biomass (litterfall), HB is consumption by herbivorous animals, HV is human harvest (if any), and residual consumption includes minor emissions such as biogenic volatile organic compounds (BVOCs) and rhizodeposition from roots (Fig. 1).

From the viewpoint of carbon balance between the atmosphere and ecosystem, NPP is defined as follows:

$$\mathrm{NPP} = \mathrm{GPP} - \mathrm{AR} \quad (2a)$$

$$= \mathrm{GPP} \times (1 - \mathrm{AR/GPP}) \quad (2b)$$

$$= \mathrm{GPP} \times \mathrm{CUE},$$

where GPP is photosynthetic carbon assimilation or gross primary production, AR is metabolic carbon consumption by autotrophic respiration, and CUE is

Correspondence: Akihiko Ito, Center for Global Environmental Research, National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan, tel. + 81 29 850 2981, fax + 81 29 850 2960, e-mail: itoh@nies.go.jp

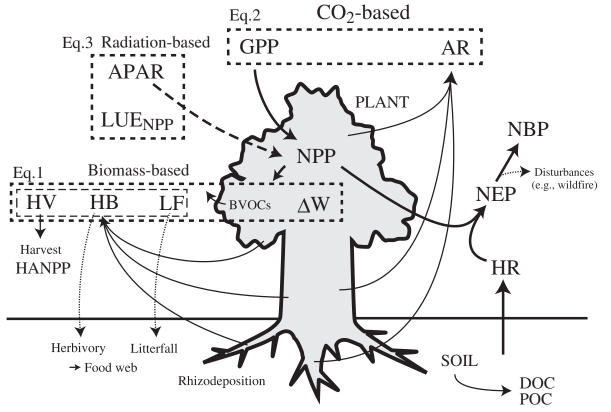

Fig. 1 Schematic diagram of terrestrial carbon cycle putting emphasis on net primary productivity (NPP). APAR, absorbed photosynthetically active radiation; AR, autotrophic respiration; BVOCs, biogenic volatile organic compounds; DOC, dissolved organic carbon; GPP, gross primary production; HANPP, human appropriation of NPP; HB, grazing by herbivores; HR, heterotrophic respiration; HV, harvest; LF, litterfall; LUE_{NPP}, light-use efficiency; NBP, net biome production; NEP, net primary production; POC, particle organic matter; and ΔW, biomass change.

ecosystem-scale carbon use efficiency (= NPP/GPP). In this sense, NPP is a conceptual parameter obtained from measurement of carbon stock and carbon flows.

NPP is calculated from the relationship between solar energy absorption and biomass production, obtained by using field and satellite remote sensing techniques (Monteith, 1972), as follows:

$$\mathrm{NPP} = \mathrm{LUE}_{\mathrm{NPP}} \times \mathrm{APAR}, \qquad (3)$$

where LUE_{NPP} is the light-use efficiency of NPP and APAR is absorbed photosynthetically active radiation. Note that this equation is sometimes defined using total shortwave radiation in place of PAR. Because most optical remote sensing observes only spectrum reflectance of the plant canopy, estimation of ecosystem-scale NPP including the carbon budget of nonassimilative organs (i.e., stems, branches, and roots) requires proper determination of LUE_{NPP}, which is affected by multiple biological and environmental factors.

Global terrestrial NPP (NPP_T) is an important parameter in terms of human appropriation and biogeochemical climate feedback, but its quantification has a long history and is still being debated. NPP_T evaluation began with the first approximation by von Liebig (1862), which was based on very limited information, but he obtained a surprisingly fair result (Ito, 2005). In the early 20th century, a few foresighted researchers (e.g., S. Arrhenius) also speculated about NPP_T in terms of climatology and geochemistry of the biosphere. After World War II, researchers focused more attention on the Earth's capacity to handle the explosive population increase, industrial development, and environmental deterioration.

From 1964 to 1974, the International Biological Programme (IBP; founded by the International Council of Scientific Unions) attempted through an unprecedented number of ecosystem surveys to evaluate the biospheric capacity to sustain the human population. In this project, field measurements were conducted for major biomes, including pristine tropical rain forest (e.g., Kira, 1987), providing researchers with invaluable data on ecosystem ecology. The first inventory synthesis of biomass and productivity at the biosphere scale (Whittaker & Likens, 1973) was achieved through the collaboration of researchers worldwide. Ajtay *et al.* (1979) and Saugier *et al.* (2001) made updated inventory-based estimates using larger field datasets. In addition, site-based data allowed researchers to construct empirical models using statistical relationships between NPP and climatological conditions (e.g., Miami model, Lieth, 1975b; Osnabrück Biosphere Model, Esser, 1987). By using an appropriate global climate dataset, the geographical mapping of global NPP distribution was realized. It is noteworthy that the global NPP distribution obtained by early studies (e.g., Lieth, 1964) is qualitatively consistent with recent estimates.

Despite these advances, it was still difficult to estimate temporal variability in NPP using such empirical approaches, especially under elevated CO_2 and global warming conditions. The next breakthrough was achieved through the development of simple, process-based models, such as Terrestrial Ecological Model by Melillo *et al.* (1993) and Biome-BGC by Running & Hunt (1993), in which NPP was evaluated while taking account of biological factors. These models enabled the estimation of temporal variability of NPP and other ecosystem processes in response to global environmental change. The International Geosphere-Biosphere Program (IGBP) was launched in 1987, and several core projects accelerated model development in conjunction with experimental studies [e.g., Data and Information System (IGBP-DIS)]. Terrestrial ecosystem models simulating more realistic processes such as vegetation dynamics and resultant biome shifts (i.e., Dynamic Global Vegetation Models, DGVMs) also have been developed (e.g., Sitch *et al.*, 2003; Woodward & Lomas, 2004; Krinner *et al.*, 2005). One of the common benchmarking tests of these models is comparison of the estimated NPP_T with the range of previous estimates.

Broad-scale vegetation remote sensing by means of satellite imagery emerged as a new research area in the 1990s. Diagnostic mapping of vegetation properties including NPP was one of the most important aims of vegetation remote sensing (Tucker & Sellers, 1986; Field *et al*., 1995). Global NPP mapping has been achieved using the LUE approach [Eqn (3)], in which APAR is estimated using empirical relationships with optically observed vegetation indices [e.g., the Carnegie-Ames-Stanford-Approach (CASA) by Potter *et al*., 1993]. Field *et al*. (1998) presented a biospheric map of NPP covering both terrestrial and oceanic ecosystems, using the CASA model and an ocean productivity model.

Although not discussed here because of space limitation, the NPP data obtained worldwide enable researchers to conduct ecologically insightful analyses focusing on the mechanisms regulating productivity (e.g., Knapp & Smith, 2001; Nemani *et al*., 2003). At present estimating NPP_T is not the only aim of global ecological studies, as the net ecosystem CO_2 budget (= NPP − heterotrophic respiration) is more directly related to atmospheric composition and climate change. Nevertheless, quantifying NPP is still an important benchmark of the quality of our ecosystem evaluation.

There is not yet a single NPP_T estimate that has achieved broad consensus among the majority of researchers (e.g., Saugier *et al*., 2001). This uncertainty results from several serious problems. First, it is still difficult to measure NPP directly at the ecosystem scale with high accuracy. For the field biometric approach [Eqn (1)], measuring ΔW is time-consuming and expensive, particularly for forests. Measurement of LF and HB is usually difficult, especially for underground components. With the flux measurement approach [Eqn (2)], it is impossible to measure NPP directly and difficult to measure GPP and AR separately, even using the eddy-covariance method and ancillary chamber measurement. When using the remote sensing approach [Eqn (3)], defining LUE to be representative at the ecosystem or broader scale is crucial, and cloud contamination and other technical difficulties often disturb accurate measurement of APAR. These difficulties in the determination and parameterization of GPP, AR, LUE, and APAR are responsible, in part, for the estimation uncertainty of process-based terrestrial ecosystem models.

I conducted a meta-analysis of NPP_T, emphasizing a historical point of view. Because I focus on global estimates, regional variability is beyond the scope of this paper. Differences in regional boundaries among studies make it difficult to conduct a region-specific meta-analysis. I gathered estimates of NPP_T mainly from scientific papers and books published from 1862 to 2011 and assessed how estimates and perceptions of the 'present' NPP_T have changed. (Note that the 'present' time varies among the publications.) Obviously, various kinds of changes have occurred during the last 140 years. Measurement and data analysis techniques have improved considerably, and the present NPP should have been affected by natural and anthropogenic environmental changes. For example, atmospheric CO_2 concentration increased from 289 ppmv in 1862 to 387 ppmv in 2010 (e.g., Keeling *et al*., 2011), resulting in NPP augmentation due to the CO_2 fertilization effect. Other factors such as climate change, nitrogen deposition, deforestation, and human appropriation have added complicated regional trends. Although it is difficult to simply compare NPP_T estimates obtained from different data sources, estimation periods, and methodologies, I show here that such meta-analysis is an efficient means of clarifying the state of our understanding of the global carbon cycle. In fact, several model-intercomparison studies (e.g., Cramer *et al*., 2001; Friedlingstein *et al*., 2006) revealed that existing models estimate somewhat inconsistent carbon cycle regimes and different responses to global change. Although previous studies recognized this uncertainty, the reasons for it were not elucidated. A historical meta-analysis of NPP_T may provide a good benchmark, because a relatively large number of estimates obtained from the pioneering work in global biogeochemistry to the present are available. Several review articles have described the existing NPP_T estimates (e.g., Lieth 1975a; Geider *et al*., 2001; Saugier *et al*., 2001), but no quantitative meta-analysis has been conducted. On the basis of my findings, I describe a possible direction to reduce or to cope with uncertainty in NPP_T estimates, especially in terms of climate projection and carbon management.

Methods

Data collection

The literature available on present NPP_T estimates was compiled. Data were extracted mainly from peer-reviewed papers and published books, found through exhaustive surveys in libraries and by on-line services with the Web of Science (Thompson-ISI, Philadelphia, PA, USA). Fundamentally, NPP_T is defined as the total NPP (i.e., global and including both aboveground and belowground fractions) of present terrestrial plants, including all natural and agricultural ecosystems. Several papers presented NPP estimates only for aboveground component, but these data were used only for ancillary analyses. This study focused on global terrestrial NPP in the context of biospheric processes and climatic feedback; regional and biome-specific analyses will be presented elsewhere.

In this study, out-dated estimates that probably used a low quantity or quality of data were also collected, because my aim was to discover the historical change in estimates of NPP_T with the development of this research field. I confirmed all NPP_T

estimates by referring to primary publications as much as possible, although later papers cited several old estimates. NPP estimates done clearly for past (e.g., preindustrial) periods and future projections were excluded from the meta-analysis. Estimation of NPP_T has been conducted using different methodologies, source data, assumptions, periods, and land areas; for example, bare ground and small islands were neglected in several studies. These differences are especially serious for model-based estimates, in which different climate, land-cover, and atmospheric CO_2 conditions were prescribed. Therefore, these assumptions were also collected from the literature. Moreover, the values of NPP_T in outstanding review articles and synthesis papers were also collected so I could assess how the state of global carbon cycle research has changed over time. Several papers presented and compared multiple values of NPP_T using different assumptions, conditions, and methods; in this case, I calculated the arithmetic mean of each study and analyzed them separately. Several estimates appeared multiple times in the literature as part of synthesis studies or for different applications of previous estimates; these overlapping values were carefully excluded from the analyses.

Publication bias is one of the most significant problems in a meta-analysis. I checked whether higher or lower estimates could be excluded to a significant degree in comparison with the level assuming an error-induced dispersion. I conducted a nonparametric test (the Kolmogorov–Smirnov test) to check normality or symmetry of the data histogram (in meta-analysis, called a funnel plot); the null hypothesis is that the data histogram shows the Gaussian distribution.

Meta-analysis: baseline

A total of 251 estimates of NPP_T were identified in 178 studies published between 1862 and 2011. The literature and estimates used in this study are listed in Table A1, which also provides additional information (e.g., periods, model names, and key assumptions). The statistical software SPSS 19 (IBM Corp., New York, NY, USA) was used to calculate statistical metrics. First, I plotted the individual estimates ($n = 251$) and publication-based mean values ($n = 178$) against the year of publication for each, showing the temporal change in the perception of the 'present' state of NPP_T. These straightforward plots illustrate how NPP_T estimates have changed along with the development of research methodology and data accumulation (Saugier *et al*., 2001; Scurlock & Olson, 2002). Also, these plots indicate how much uncertainty remains in the current evaluation of global NPP and the carbon cycle. Using the historical data, I calculated the median and variance using cumulative past estimates for each year (e.g., the statistics for 2000 were calculated using data published from 1862 to 1999). Stability of the median and decreasing variance are expected to indicate convergence of the community's perception of NPP_T. To further clarify the temporal change in NPP estimates, statistics (average, median, maximum, minimum, standard deviation [σ], 95%-confidence interval, kurtosis, skewness, and quartiles) were calculated for estimates published from 1960 to the 2011, at 10-year intervals.

The 251 estimates were classified on the basis of methodology, with the following five categories of estimation method considered:

(I) Inventory: statistical aggregation of observational data. Typically, field observational data collected worldwide are classified on the basis of biome type and averaged to obtain areal-mean annual NPP for each biome. Then, the mean values are multiplied by biome area to obtain biome-total NPP, and the summation for all biomes gives the biospheric NPP_T. It should be noted, however, that the data aggregation estimates in different papers may not be truly independent of each other, because common observational data could be used cumulatively through time.

(II) Empirical model simulation: field data of annual NPP values are commonly correlated with site-specific environmental indices, such as annual mean temperature and annual precipitation, using appropriate equations. Then, the empirical NPP models are applied at global scale using appropriate input data (e.g., climate field) to obtain NPP_T.

(III) Biogeochemical model simulation: ccosystem-scale carbon cycle models are developed to simulate carbon flows such as photosynthesis, respiration, and decomposition, taking account of ecophysiological differences among biomes (e.g., photosynthetic capacity and environmental responsiveness). Then, global simulations are conducted using the models and appropriate input data (e.g., climate, land cover, and soil) to obtain NPP_T and other carbon-related properties.

(IV) Dynamic global vegetation model simulation: DGVMs simulate NPP using equations similar to those of biogeochemical models, as well as long-term change in vegetation structure. Therefore, these dynamic vegetation models are more prognostic than the biogeochemical models; however, they can contain intrinsic uncertainty in the accuracy of the current land-cover distribution.

(V) Remote-sensing estimation: in this approach, at least some key vegetation properties [e.g., fraction of APAR and leaf area index (LAI)] determining NPP are derived from satellite remote-sensing observations. The relationship between absorbed solar radiation and NPP [Eqn (3)] is frequently used.

For each of the five categories containing data from different publication years, statistical metrics were calculated and analysis of variance (ANOVA) was conducted to analyze the significance of difference among the methods. Note that (1) several empirical and biogeochemical model simulations used land-cover data derived from satellite remote sensing but were not classified as remote-sending estimation; (2) the model-based NPP_T estimates were derived using models with different degrees of complexity; and (3) remote-sensing-based estimations may use models to evaluate biological controls. Therefore, a sensitivity analysis (described later) was conducted to assess the impact of uncertainty in methodological categorization.

Ancillary analyses

Ancillary analyses were conducted using the data and additional information from the literature. First, interannual variability in NPP_T was compared among the studies available for this analysis. Time-series, linear trend, and amplitude of the interannual variability were considered. Second, I examined the variability of NPP_T estimates in model-intercomparison papers. Because common simulation protocols and input data were used in the model-intercomparison studies, this analysis is expected to reveal variability stemming solely from the differences among models. Third, the time-series of NPP_T values estimated by several representative models were examined. Several models presented multiple estimates of NPP_T differing in simulation period, input data, and model development stage (i.e., model version). Fourth, several ecologically interesting features were briefly examined: CUE of the biospheric NPP (i.e., NPP_T/GPP_T ratio), contributions of C_3 and C_4 photosynthetic pathways, human appropriation of NPP, and comparison with the preindustrial NPP_T estimated using models and preindustrial conditions (e.g., atmospheric CO_2 concentration is typically assumed to be 280 ppmv).

Sensitivity analyses

In addition to the baseline analysis, sensitivity analyses were conducted to examine robustness of the meta-analysis. First, the statistical metrics were recalculated (1) after removing outlier (outside the range of $\pm 2\sigma$) estimates, and (2) after randomly separating the entire sample into two subsamples repeatedly (i.e., the half-split method). Because estimates used in the meta-analysis may not be independent of each other in terms of basic field data and methodology, such an examination of the sample-size reduction is meaningful. Second, the number of methodological categories was reduced (the three model-based categories were aggregated into a single category and biogeochemical models and remote-sensing studies were merged into a single category), and then the statistical metrics were recalculated. Third, the statistical metrics were recalculated after weighting values with the inverse of the age of publications. Here, to obtain the statistics, all estimates were weighted as follows:

$$NPP_{weighted} = NPP \exp[k(PY - 2010)], \quad (4)$$

where k is the attenuation coefficient and PY is publication year. For example, when $k = -0.1$ (or -0.01), an estimate with $PY = 1980$ is weighted by 0.135 (0.819) compared with that with $PY = 2010$. This manipulation results in heavier weight for newer studies and lighter weight for older studies, with the assumption that recent studies using advanced methodology and data have greater credibility.

Results and discussion

Overview of all estimates

The 251 estimates of NPP_T extracted from the literature published between 1862 and 2011 ranged from 10.3 to 149 Pg C yr^{-1}, with mean and median value of 56.2 and 56.4 Pg C yr^{-1}, respectively, with a standard deviation $\sigma = 14.3$ Pg C yr^{-1}. The overall degree of variability seems huge, as only 52.2% of the data is within the mean $\pm 0.5\sigma$. The mean and median values of the estimated NPP_T are similar to those presented in synthesis articles on the global carbon cycle (Table 1). A publication bias was revealed by the histogram including all estimates (Kolmogorov–Smirnov test, $P = 0.010$), due to low values published before the IBP period, as mentioned below. However, for the post-IBP estimates (after 1980, $n = 220$), no significant publication bias was found (i.e., the distribution fits the Gaussian distribution, $P = 0.117$). For the post-IBP data, the 95% confidence interval of NPP_T estimates was 36.3–80.1 Pg C yr^{-1}.

Temporal variation, 1862–2010

Starting with the attempt by von Liebig (1862), numerous and various estimates of the 'modern' or 'present' NPP_T have been published (Fig. 2). Estimates from before 1960, which were based on the inventory method, had lower values (10–30 Pg C yr^{-1}) because of the lack of observational evidence from fertile ecosystems such as tropical rain forest. Only seven estimates were published before 1960, none of which was intended to specifically quantify the NPP_T. During the IBP period (1964–1974), a substantially wide range of NPP_T estimates were published, including several high values (e.g., ~ 106 Pg C yr^{-1}), probably because of the awareness of highly productive ecosystems on Earth. Clearly,

Table 1 Published values of present terrestrial net primary productivity (NPP_T) in milestone review papers

Reference	NPP_T (Pg C yr^{-1})
Bolin (1970)	25
Woodwell *et al.* (1978)	52.8
IPCC 1st Assessment Report (1990), fig. 1.1	52
Siegenthaler & Sarmiento (1993)	51.97
Sundquist (1993)	60
IPCC 2nd Assessment Report (1996), fig. 2.1	61.3
Schlesinger (1997)	60
Schimel *et al.* (2001) after Cramer *et al.* (1999)	42–68
Geider *et al.* (2001)	56.4
IPCC 3rd Assessment Report (2001), fig. 3.1	60
Gruber *et al.* (2004)	57
IPCC 4th Assessment Report (2007), fig. 7.3 etc.	Value not shown

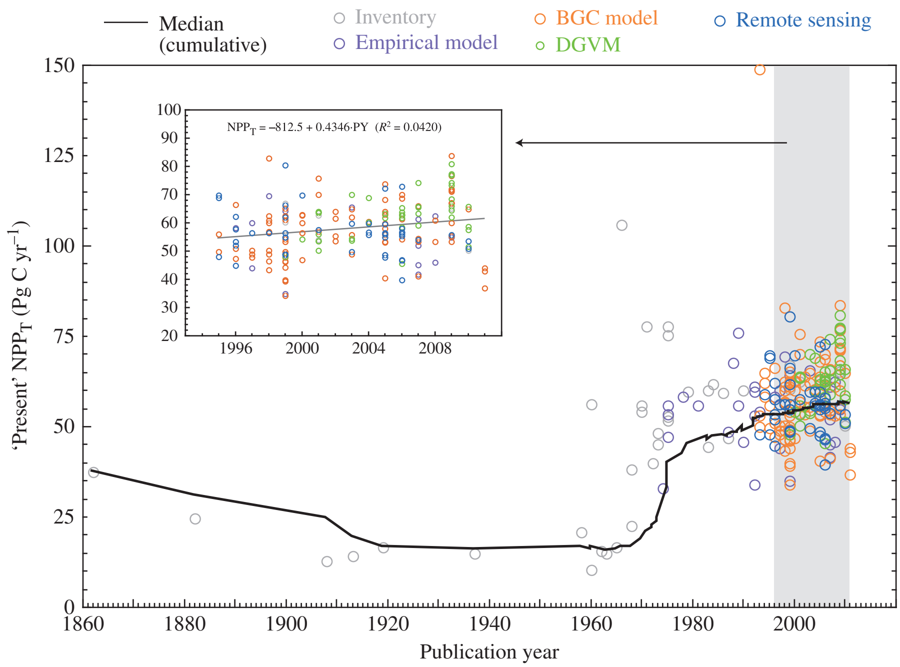

Fig. 2 Temporal change in global terrestrial net primary productivity (NPP$_T$) plotted for individual estimates against the year of publication. Note that the 'present' time varies among the publications. Medians of the historically cumulative values are shown. Inset, data after 1995 are shown with linear regression.

Table 2 Statistical metrics of the estimated global terrestrial net primary production published in the literature during various periods

	Periods						
Metric	Unit	1862–2011	1960s	1970s	1980s	1990s	2000s
Sample	No.	251	8	16	10	76	134
Mean	Pg C yr^{-1}	56.2	35.1	55.4	57.7	56.0	59.5
Standard deviation	Pg C yr^{-1}	14.3	32.5	12.7	9.7	14.3	8.9
Kurtosis	–	8.2	3.19	0.07	−0.02	23.44	0.02
Skewness	–	0.45	1.82	0.49	0.45	3.74	0.04
Maximum	Pg C yr^{-1}	149.0	106.0	77.6	76.0	149.0	83.8
75% quartile	Pg C yr^{-1}	63.0	42.9	58.6	61.4	61.1	65.0
Median	Pg C yr^{-1}	56.4	19.6	53.8	57.7	54.6	59.8
25% quartile	Pg C yr^{-1}	49.5	15.5	48.0	50.4	48.5	54.0
Minimum	Pg C yr^{-1}	10.3	10.3	33.1	44.6	34.0	37.0

the NPP$_T$ values presented by the IBP synthesis exerted a strong influence, because there were the first results based on extensive measurements using a standardized method. The trajectory of the median of historically cumulative NPP$_T$ (black curve in Fig. 2) shows the impact; the median rapidly increased during the IBP period and then gradually stabilized at a level around 55 Pg C yr^{-1}. The inventory-based estimates after the IBP period generally converged around that value: for example, 52.9 Pg C yr^{-1} by Whittaker & Likens, (1975) and 59.9 Pg C yr^{-1} by Ajtay *et al*. (1979). Next, a wave of papers containing NPP$_T$ estimates based mainly on models and remote-sensing approaches were published: 76 estimates in the 1990s and 134 estimates between 2000 and 2011 (Table 2). These estimates were model-based and more or less calibrated using observational data, but substantial variability remains (σ, ± 14.3 and ± 8.9 Pg C yr^{-1} for the two sets of estimates, respectively), probably due to insufficient observational data and the lack of appropriate parameter optimization algorithms. Note that Fig. 2 includes multiple estimates from single papers (e.g., model-intercomparison papers); see Figure A1 for the plot of paper-based values.

In the entire dataset as well as in relatively recent data (1995–2011, Fig. 2, inset), there was an incremental trend with a slope of 0.43 Pg C yr^{-1}; this trend is statistically significant as examined by Mann–Kendall test at a confidence level of 95% ($\tau = 0.179 > \tau_{g(95\%)} = 0.0944$) but seems weak due to scattering of the estimates. It is premature to attribute this increasing trend in the estimated NPP_T to specific global phenomena such as elevated CO_2 concentration and climate change, during the period. For instance, several model-based studies published after 2000 provide high estimations of NPP_T, and these studies used different forcing data derived from climate models.

Comparison among estimation methods

The statistical metrics of NPP_T estimated by different methods are compared in Table 3. The inventory- and DGVM-based simulations estimated the lowest (median, 50.3 Pg C yr^{-1}) and highest NPP_T (median, 62.6 Pg C yr^{-1}) respectively. The difference among methods was statistically significant, according to ANOVA using the Kruskal–Wallis test ($P < 0.05$). Note that most of the estimates using the data aggregation method were conducted before 1980 and obtained by Eqn (1), whereas most model-based estimates were published after 1990 and obtained by Eqns (2) or (3). Figure 3 shows the histogram of NPP_T estimated by the five methods. Values based on the inventory method are dispersed from the lowest to the highest end, implying they were based on insufficient observational data and a standardized aggregation method. Again, the extensive surveys by the IBP (Whittaker & Likens, 1975) and SCOPE (Ajtay *et al.*, 1979) considerably improved convergence of the NPP_T estimates.

More extensive datasets of observed NPP are now available. For example, the Global Primary Production Data Initiative (GPPDI; Scurlock *et al.*, 1999; Olson *et al.*, 2001; data available at http://daac.ornl.gov/) established a dataset including high-quality (i.e., obtained by intensive surveys or well-documented) data from 162 sites and extensive 0.5° mesh data at 5162 grid points. The GPPDI dataset contains NPP data, for example, from 27 tropical evergreen forests and 56 evergreen conifer forests. Correspondingly, the accuracy of estimates based on the empirical models was improved by using more observational data and a deeper understanding of terrestrial ecosystems. For example, Zaks *et al.* (2007) developed the Madison

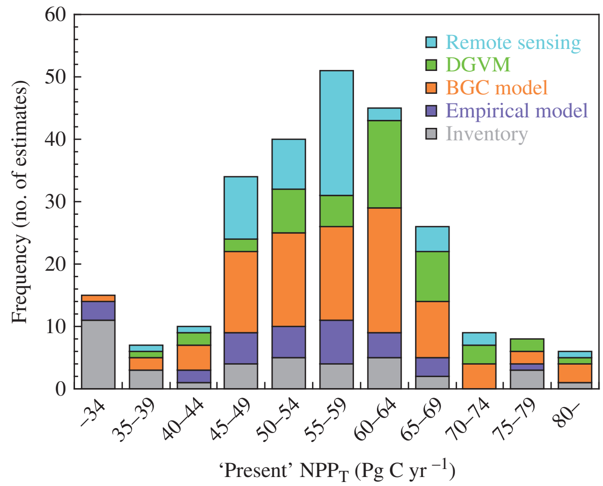

Fig. 3 Histogram of the 251 estimates of global terrestrial net primary productivity (NPP_T), categorized into five groups according to estimation methods.

Table 3 Statistical metrics of the estimated global terrestrial net primary production estimated by various methods in the literature

		Estimation method				
Metric	Unit	Inventory aggregation	Empirical model	BGC model	DGVM	Remote sensing
Sample	No.	39	30	88	45	49
Mean	Pg C yr^{-1}	46.2	54.0	58.8	61.2	56.4
Standard deviation	Pg C yr^{-1}	22.3	10.5	13.7	9.4	7.9
Kurtosis	–	−0.13	−0.15	20.81	0.24	1.17
Skewness	–	0.11	−0.24	3.30	−0.31	0.82
Max	Pg C yr^{-1}	106.0	76.0	149.0	81.0	80.5
75% quartile	Pg C yr^{-1}	60.2	60.9	64.0	65.8	59.0
Median	Pg C yr^{-1}	50.3	55.5	57.5	62.6	56.0
25% quartile	Pg C yr^{-1}	23.5	46.3	50.3	54.5	51.0
Min	Pg C yr^{-1}	10.3	33.1	34.2	37.0	39.7

BGC model, biogeochemical model; DGVM, dynamic global vegetation model.

model of empirical NPP_T estimation as a function of annual temperature, precipitation, and radiation, using 3023 field data points. However, the present NPP datasets are likely still insufficient. In the GPPDI, few field data on NPP in pasture and tundra/desert are included and the mesh data covers only about 10% of the total land area. Also, the fact that field surveys were conducted in different time periods causes problems, such that differences in atmospheric CO_2 levels and climate conditions must be accounted for (discussed later).

Biogeochemical and dynamic vegetation modeling studies have provided a wide range of NPP_T estimates, because of a combination of differences in simulation design, forcing/calibration data, and model sensitivity. For example, the model intercomparison study by Cramer *et al*. (1999) revealed a wide range of variability in NPP_T (39.9–80.5 Pg C yr^{-1}; when outliers are excluded, 44.3–66.3 Pg C yr^{-1}) among 17 terrestrial models. According to their spatial analysis (numerical data included in the International Satellite Land Surface Climatology Project Initiative II dataset; Hall *et al*., 2006), standard deviation (absolute variability) among the 17 estimates was large in southeastern South America, the Andes, western Europe, central Africa, southern East Asia, and part of Southeast Asia (figure not shown). In contrast, the coefficient of variation (CV, standard deviation divided by mean, that is, the relative variability) of the 17 estimates was large in low-productivity areas such as arctic tundra and sand deserts in North Africa (Sahara) and Central Asia. In conjunction with the observation-based NPP map from the GPPDI data, I found that most of the high-uncertainty areas lack field evidence, which would help constrain model evaluations. Also, Ito & Sasai (2006) systematically conducted simulations using two ecosystem models and three climate datasets, and found that differences in both model and data were responsible for the difference in estimated NPP_T (39.7–63.0 Pg C yr^{-1}). Reducing the uncertainty is still difficult, however, because a substantial degree of variability remains in the time-series plot even in recent years.

Many estimates derived using the remote-sensing approach were based on a few common global data of vegetation properties such as vegetation greenness indices (e.g., normalized difference vegetation index), LAI, and fraction of APAR observed by the Advanced Very High Resolution Radiometer (AVHRR) aboard a NOAA satellite and Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Terra and Aqua satellites. Nevertheless, these estimates exhibit a substantial range of variability (SD = 7.9 Pg C yr^{-1}) comparable with that of the DGVM approach. This variability may be attributable to differences in satellite products, study periods, climate data, and NPP estimation schemes. For example, Nemani *et al*., (2003) derived quite different NPP_T values for the period 1982–1999 using two NOAA/AVHRR products (GIMMS and PAL) differing in atmospheric correction for aerosols and other factors, but using the same NPP estimation algorithm, 49.98 Pg C yr^{-1} by GIMMS and 59.74 Pg C yr^{-1} by PAL.

For many of the inventory- and model-based estimates, difference in total land area and biome coverage may at least partly explain the variability in the NPP_T estimates. The total land area assumed in the literature ranged from $106.2 \times 10^6\,km^2$ (Kohlmaier *et al*., 1997) to $149.3 \times 10^6\,km^2$ (Saugier *et al*., 2001). Although notable differences in NPP may arise mainly owing to low-productivity areas such as polar deserts and small islands, the difference in total land area should be taken into account. Tendencies found in area-average NPP can be different from those in the total NPP_T. For example, area-average NPP estimated by Kohlmaier *et al*., (1997), 473.4 g C $m^{-2}\,yr^{-1}$ (NPP_T, 50.3 Pg C yr^{-1}), is much higher than that estimated by Saugier *et al*., (2001), 419.3 g C $m^{-2}\,yr^{-1}$ (NPP_T, 62.6 Pg C yr^{-1}). Also, difference in the latitudinal gradient of calculated mesh area (e.g., due to difference of spheroids used for global aggregation; Oki & Sud, 1998) could influence the NPP_T evaluation, such that high-productivity tropical forests and low-productivity arctic rangelands are multiplied by different areal weights. Differences in land-cover data (e.g., forest, pasture, and cropland areas) affect NPP_T evaluation when using the inventory-based (Saugier *et al*., 2001) and model-based methods (e.g., DeFries *et al*., 1999; Jain & Yang, 2005), because of inconsistencies in areal weighting and parameter values for each biome. Even for DGVM-based estimates, static/dynamic simulations and on-line/off-line (i.e., coupled or uncoupled with climate model) simulations can provide different land-cover and NPP_T estimates (e.g., Delire *et al*., 2003; Krinner *et al*., 2005). Therefore, reducing the uncertainty in land-cover map by using some continuous parameterization and scaling-up approaches would improve the accuracy of NPP_T and global carbon budget estimation.

Ancillary analyses

Interannual variability. Interannual variability in NPP_T differed among the available time series data (Fig. 4). Early studies (e.g., Maisongrande *et al*., 1995) estimated larger amplitude of variability, probably because they used parameterizations with higher responsiveness to vegetation index and climate conditions. Ito & Sasai (2006) showed that difference in solar radiation among climate data sets and in model sensitivity to solar radiation have large impacts on the variability among

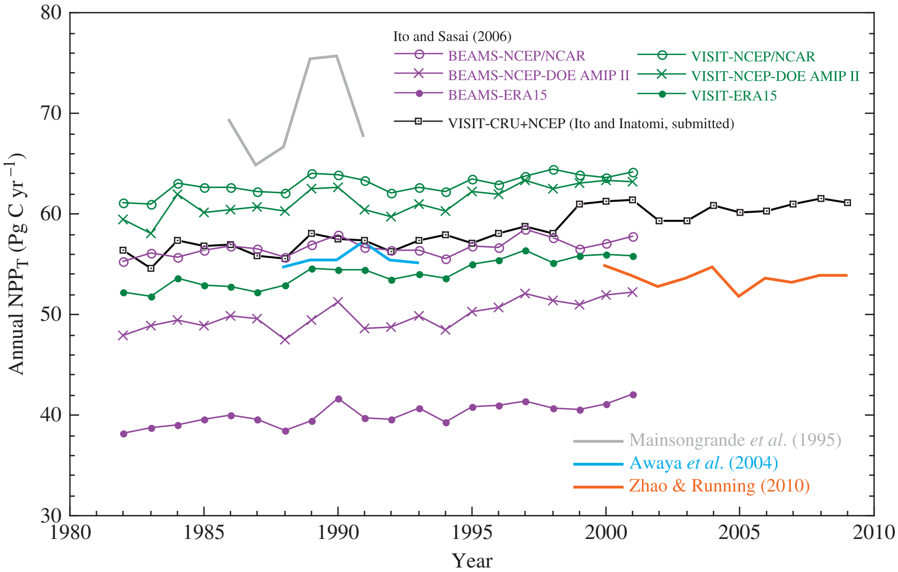

Fig. 4 Interannual variability in the estimated global terrestrial net primary productivity (NPP$_T$). Time-series of BEAMS and VISIT (formerly Sim-CYCLE) models using different climate data were obtained from Ito & Sasai (2006). Data using the VISIT model and the CRU climate dataset (A. Ito and M. Inatomi, unpublished data) are also shown.

estimates. Similarly, the magnitude of the linear trend was different among estimates. For example, Nemani *et al*. (2003) obtained linear trends in NPP$_T$ at +0.23 (Pg C yr^{-1}) yr^{-1} using GIMMS data and +0.12 (Pg C yr^{-1}) yr^{-1} using PAL data during the period 1982–1999. Ito & Sasai (2006) also obtained different linear trends in NPP$_T$ using multiple models and climate data, ranging from +0.08 to +0.21 (Pg C yr^{-1}) yr^{-1} during the period 1982–2001. Although each time-series of NPP$_T$ shows an incremental trend mainly due to rising atmospheric CO_2 and climate change, such a difference in magnitude is critical when considering ecosystem responses and feedbacks to global changes.

NPP change from the pre-industrial period. By assuming the preindustrial conditions of atmospheric CO_2 concentration (typically 280 ppmv), climate, and land-cover, several studies have attempted to estimate the pre-industrial NPP$_T$ ($n = 24$). For example, François *et al*. (1998), using the CARAIB model, estimated the preindustrial NPP$_T$ as 54.6 Pg C yr^{-1} for the actual vegetation distribution, which is 10% lower than the estimated NPP$_T$ under the present condition (62.5 Pg C yr^{-1}). Sitch *et al*. (2003), using the LPJ model, estimated the pre-industrial and present NPP$_T$ as 64 and 70 Pg C yr^{-1}, respectively. Arora & Matthews (2009) reported the preindustrial (atmospheric CO_2 at 280 ppmv) and present (365 ppmv) NPP$_T$ estimated by 13 terrestrial models coupled with climate models. They showed that NPP$_T$ at the present atmospheric CO_2 level is higher than the preindustrial NPP$_T$ by 7%–30% (median, 15.5%). Using ORCHIDEE model, Piao *et al*. (2009) showed that NPP$_T$ increased from 67.5 Pg C yr^{-1} in 1901 to 77.0 Pg C yr^{-1} in 2002. Although little direct evidence has been presented on the preindustrial NPP$_T$, the model studies imply that the preindustrial value is lower than the present value because of the lower atmospheric CO_2 concentration and changes in climate conditions. Note that local NPP decline caused by land-use conversion and ecosystem degradation (e.g., globally, –4 to –10% of NPP due to soil degradation; Zika & Erb, 2009) might have offset the global NPP$_T$ enhancement.

Intermodel variability

Revealing the degree of uncertainty in estimates is one of the objectives of model-intercomparison research (e.g., Cramer *et al*., 1999). Because the simulations in these intercomaprison studies were conducted using common input data to isolate the model-attributed difference, it is expected that the range of variability will be smaller than that obtained from meta-analyses including a variety of studies. Figure 5 shows the distribution of estimated NPP$_T$ obtained from the model-intercomparison papers, in which multiple estimates were compared. The results indicate, in general, the existence of a wide range of variability. For example, the 17 estimates of NPP$_T$ in Cramer *et al*. (1999) have standard deviation of 10.4 Pg C yr^{-1} (excluding outliers, 7.7 Pg C yr^{-1}). Arora & Matthews (2009) reported a comparable range of variability among 13 models; note

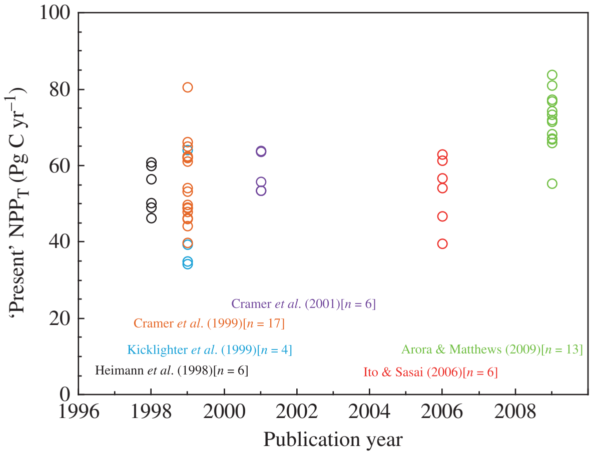

Fig. 5 Temporal change in the global terrestrial net primary productivity (NPP_T) obtained from model-intercomparison papers.

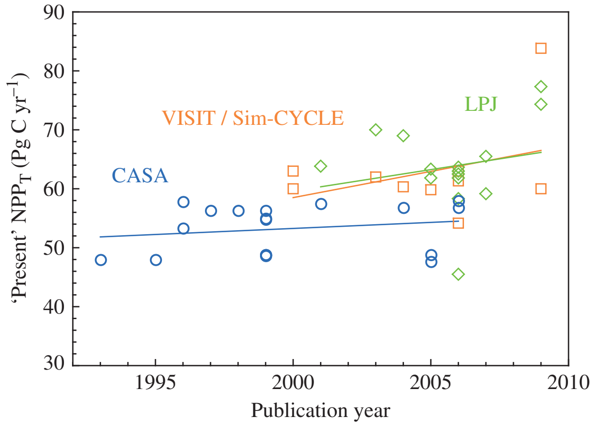

Fig. 6 Temporal change in the global terrestrial net primary productivity (NPP_T) estimated by three models: CASA, VISIT (formerly, Sim-CYCLE), and LPJ.

that their estimates were obtained from coupled climate–carbon cycle models (i.e., model-specific biases in climate condition may remain) at an atmospheric CO_2 level of 365 ppmv.

Intramodel variability. Several models used in different studies provided multiple NPP_T estimates. Because of differences in simulation configuration and model developmental stage (version), estimates derived using the same modeling approach are not always identical. Figure 6 shows the distribution of NPP_T estimated by three representative models: CASA, LPJ, and VISIT (formerly called Sim-CYCLE). Estimates by CASA seem relatively stable, probably because these values are derived from and then constrained by remote sensing data. In contrast, the biogeochemical model VISIT and the dynamic vegetation model LPJ resulted in widely variable NPP_T estimates in different papers, because these types of models are only loosely constrained by observed land surface properties. For example, higher NPP_T values were obtained when VISIT/Sim-CYCLE and LPJ were coupled with climate models (e.g., Arora & Matthews, 2009).

CUE of NPP_T. Several studies estimated total annual GPP (GPP_T) as well as NPP_T using data synthesis (Fogg, 1958; Golley, 1972) and models (e.g., Box, 1978; Delire *et al.*, 2003). In this meta-analysis, I examined 29 estimates of CUE (i.e., NPP_T/GPP_T). The ratio is broadly assumed to be about 0.5 because about half of photosynthate may be consumed by plant respiration. The global-scale CUE value differed among studies, ranging from 0.326 to 0.875 (median = 0.476). In general, higher values of GPP_T ($\sim 130\,\mathrm{Pg\,C\,yr^{-1}}$) resulted in lower values of CUE, because NPP_T was rather stable among the studies. A meta-analysis by DeLucia *et al.* (2007) indicated that the mean CUE derived from all forest data was 0.53 (0.23–0.83 for different forest types). Similarly, Ise *et al.* (2010) obtained the global-mean CUE of forested ecosystems: 0.442 by a meta-analysis and 0.403–0.466 by modeling approaches. The NPP/GPP ratio is variable in relation to biome type, biomass, stand age, and climate condition (Waring *et al.*, 1998; Piao *et al.*, 2010).

C_3 and C_4 contributions. The individual contributions of C_3 and C_4 photosynthetic pathways to NPP_T were estimated only by biogeochemical and dynamic vegetation models, because such calculations are difficult for inventory and remote-sensing studies. For example, François *et al.* (1998) estimated the NPP_T and the contributions of C_3 and C_4 plants at the modern and during the Last Glacial Maximum using the CARAIB model; they found that $14.5\,\mathrm{Pg\,C\,yr^{-1}}$ (23.2% of the NPP_T of $62.5\,\mathrm{Pg\,C\,yr^{-1}}$) was from the C_4 photosynthetic pathway during the modern period. Using the CASA-model framework, Still *et al.* (2003) estimated total NPP by C_4 grasses on the basis of the ecophysiological relationship of LUE as $13.6\,\mathrm{Pg\,C\,yr^{-1}}$ (27.8% of the NPP_T of $48.9\,\mathrm{Pg\,C\,yr^{-1}}$). Because the C_3- and C_4-photosynthetic pathways have different resource-use efficiencies and degrees of environmental responsiveness, it is important to conduct separate evaluations of their contributions on the basis of appropriate biogeographical information.

Human impacts. Human appropriation of NPP (HANPP) is one of the indices of human impacts on the biosphere and includes harvest and exploitation of food, timber, fuel wood, fiber, meats, and so on (e.g., Imhoff *et al*., 2004; Haberl *et al*., 2007). The data regarding these products, including residues and debris, are insufficient, such that estimation uncertainties remain in the amount of HANPP. Imhoff *et al*. (2004) estimated that 14.1–26.07% of NPP_T (56.8 Pg C yr^{-1} according to the CASA model) is consumed by human activities. Haberl *et al*. (2007) estimated that 23.8% of NPP_T (65.51 Pg C yr^{-1} according to the LPJ model for potential vegetation) is consumed by human activities, including human-caused fires. The estimated fractions of human appropriation ($HANPP/NPP_T$) are considerable, but the values are susceptible to the uncertainty in NPP estimation. Also, these human appropriation studies estimated the potential NPP_T (i.e., productivity without human impacts such as land-use conversion). Vitousek *et al*. (1986) and Haberl *et al*. (2007) estimated the potential NPP_T as 74.8 and 65.51 Pg C yr^{-1}, respectively, implying that human activities reduce the NPP_T by 10.6–14.1% at the present time. Doughty & Field (2010) implied that agriculture has decreased NPP_T by ~ 6 Pg C yr^{-1} through restriction of effective growing period and land degradation, although management practices have ameliorated these impacts. In addition, O'Neill & Abson (2009) estimated NPP in parks and urban areas at the global scale, implying that about 14% of HANPP occurs in these protected areas.

Sensitivity analysis

The robustness of the statistical metrics obtained in the baseline analysis was examined first by conducting a sensitivity analysis, in which outlier data outside the range between $\pm 2\sigma$ (standard deviation of all data) were excluded. As a result, 13 estimates that might be based on insufficient data but were influential in statistical analyses were removed. Although standard deviation among the remaining 238 estimates became narrow ($\pm$ 9.7 Pg C yr^{-1}), the mean and median values (57.5 and 56.8 Pg C yr^{-1}) were similar to those of the baseline analysis using all data. When the entire data set was randomly separated into two subsamples repeatedly, similar statistical metrics were obtained from these subsamples, a finding that also implies the robustness of the baseline analysis. For example, the median value from the subsamples fell within the range 56.0–58.4 Pg C yr^{-1} and the standard deviation was between 13.5 and 15.0 Pg C yr^{-1} (cf. Table 2).

For the second sensitivity analysis, some methodological categories were merged, because the definition of estimation methods can be different according to each person's subjective point of view. For example, several dynamic vegetation models include biogeochemical processes and several remote-sensing methods contain some empirical and process-based schemes (e.g., CASA model including soil carbon dynamics). First, model-based estimates (empirical, biogeochemical, and dynamic vegetation; $n = 163$) were merged into a single category representing a broad spectrum of model studies. The mean, median, and standard deviation were obtained as 58.6, 58.8, and 12.3 Pg C yr^{-1}, respectively. Second, estimates obtained by biogeochemical models and remote sensing studies were merged into a single category ($n = 137$), which represents diagnostic and mechanistic evaluation of the current state of the biosphere. As a result, the mean, median, and standard deviation were obtained as 58.0, 56.4, and 12.0 Pg C yr^{-1}, respectively. These results indicate that the baseline analyses (Table 3) are robust against variability in the categorization of methods.

Next, I conducted a sensitivity analysis, in which data were weighted by the length of time from publication to the present [Eqn (4)], because older and more recent estimates may differ in credibility due to methodological quality. For example, recent studies may be based on more observational data, including those obtained by means of advanced instruments. As a result, weighted averages of NPP_T were obtained as 58.9 and 57.1 Pg C yr^{-1} for the case of $k = -0.1$ and -0.01, respectively. The difference caused by this time-dependent weighting is not particularly large compared with the range of standard deviations among studies (i.e., statistically insignificant), supporting the robustness of the statistical metrics obtained in the baseline analysis (Tables 2 and 3).

Concluding remarks

This study investigated the historical development of our understanding and quantification of the global biogeochemical cycle, considering the case of NPP of the terrestrial biosphere. A historical meta-analysis provides a more comprehensive perspective on this matter, compared with previous descriptive reviews (e.g., Lieth 1975a; Geider *et al*., 2001; Saugier *et al*., 2001). This analysis suggested that a representative value (median) of global terrestrial NPP is 56.4 Pg C yr^{-1}, on the basis of various estimates derived from observations, syntheses, and model-based research. The IBP contributed to a convergence of the present estimates of NPP_T, because prior studies were based on very limited data. However, it has been difficult to reduce the degree of uncertainty; for estimates published between 2000 and 2010, the variability among estimates remains at $\pm$ 8–9 Pg C yr^{-1}. This finding implies that a level of uncertainty by about $\pm 15\%$ of CV is inevitable in our evaluation of the global biogeochemical carbon cycle, including the carbon cycle feedback to climate change (e.g., Friedlingstein *et al.*, 2006).

During the last decades, field measurement instruments and techniques have advanced substantially. In addition, cumulatively increasing field data are available for estimation of NPP not only for aboveground components but also for belowground biomass and turnover. For example, optical tree-height meters and portable scales make biomass measurements in the field easier and more accurate (e.g., Clark *et al.*, 2001; Scurlock & Olson, 2002). Belowground measurement systems, such as the minirhizotron, enable the observation of root growth and turnover in a nondestructive manner (Johnson *et al.*, 2001). Recent developments in computers and the internet are apparently beneficial for the storage, exchange, management, and statistical analysis of observational data.

Nevertheless, it is still not an easy task to measure biomass, turnover, and browsing/grazing of actual ecosystems, especially well-developed forest ecosystems. Most field surveys lack observation of BVOC emission and rhizodeposition (e.g., exudation and consumption by root mycorrhizae), leading to a leakage of carbon [residual consumptions in Eqn (1)] and therefore potential underestimation of NPP by the inventory- and model-based approaches. In this sense, biogeochemical and dynamic vegetation models are insufficient in capturing belowground processes including size-dependent root turnover and carbon supply to soil microbes (Jackson *et al.*, 2000; Ostle *et al.*, 2009). These problems may account for part of the discrepancy between inventory-based NPP estimates [Eqn (1)] and model-based NPP estimates [in most cases obtained by Eqn (2)].

It is necessary to develop a more reliable method for scaling measurements to ecosystems and the biosphere (Scurlock *et al.*, 1999). Most ecosystem-scale surveys assume some allometric relationship (e.g., between diameter at breast height and trunk volume) to derive biomass from a limited number of sample measurements. Such indirect evaluation can bring about a certain magnitude of errors and biases, which propagate to ecosystem-level NPP and then NPP_T estimation. The recent development of the metabolic scaling theory (e.g., Enquist *et al.*, 2007; West *et al.*, 2009) is expected to allow more accurate scaling-up from measured properties to ecosystem-level NPP. Problems also occur in the scaling from ecosystem to the terrestrial biosphere. For successful scaling, each point-scale observation is expected to represent accurately the region or the biome it belongs to, or it is expected to be randomly sampled from the population of the global NPP distribution. Unfortunately, this may not be the case for inventory-based NPP_T estimation, because a majority of these field studies were conducted in well-preserved ecosystems to reduce the effects induced by unexpected disturbances and human impacts. Although the NPP of mature ecosystems is temporally rather stable against developmental stage (Kira & Shidei, 1967; Pregitzer & Euskirchen, 2004), young or degraded ecosystems can have much higher or lower NPP than a mature ecosystem. Most inventory-based NPP_T estimates have accounted for differences among biome types but ignore the influence of developmental stage; this is also the case for most model-based estimates. To reduce the bias, additional observational data and advanced horizontal scaling-up methods are required. Fortunately, great improvements are being made by recent efforts to up-scale flux data from a limited number of sites to the global scale through advanced use of remote sensing data (e.g., Jung *et al.*, 2009; Beer *et al.*, 2010) and to achieve spatially explicit mapping of stand age (e.g., Pan *et al.*, 2011).

With the aim of quantifying the global carbon cycle, NPP estimates have been published using some models and satellite remote-sensing data. However, I found that these estimates were inadequately constrained by observational data, leading to a substantial range of estimate dispersion. Because model simulation results are susceptible to forcing-data quality and parameter values, which cannot be adequately constrained by observations, it is difficult to reduce the uncertainty in model-based estimates. Cramer *et al.* (1999) and associated model-intercomparison analyses (e.g., Churkina *et al.*, 1999; Ruimy *et al.*, 1999) contributed substantially to clarifying the degree of uncertainty in model-based estimation. In fact, 97.0% (i.e., 130 out of 134) of estimates published after 1999 fall within the range among the 17 models analyzed by Cramer *et al.* (1999). The range of variability might prevent estimates outside the range from being published, although I have confirmed that the NPP_T estimates published between 1990 and 2010 do not show apparent publication bias. The development of parameter-optimization techniques (i.e., data-assimilation; Rayner *et al.*, 2005) is expected to reduce inter-model variability, on the condition that adequate observational data are available and used properly.

Gross fluxes [GPP and ecosystem respiration (RE)] and net ecosystem production (NEP = GPP−RE) are gaining increasing attention in terms of the terrestrial CO_2 budget, certainly due to the progress of micrometeorological flux measurement techniques (e.g., Wofsy *et al.*, 1993; Baldocchi *et al.*, 2001; Luyssaert *et al.*, 2007). It is difficult to derive NPP directly from the micrometeorological flux data for several technical reasons For example, separating RE into autotrophic and heterotrophic components with high accuracy is still difficult. Physiologically, two metabolic processes (photosynthesis and respiration) with different degree of environmental responsiveness determine NPP, making it somewhat complicated to relate it with environmental factors, which is not the case with gross fluxes. In fact, the diagram of the global carbon cycle in the 4th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2007, fig. 7.3) shows only GPP, RE, and land-use-induced emission for the terrestrial CO_2 exchange.

So, does this mean that NPP is no longer important in carbon cycle research? Clearly, the answer is No. First, NPP is still a key parameter in biometric field surveys of ecosystem carbon cycles, which are frequently used to crosscheck flux measurement results (e.g., Curtis *et al*., 2002; Miller *et al*., 2004; Luyssaert *et al*., 2009; Ohtsuka *et al*., 2009). The magnitude of NPP_T is about seven times that of anthropogenic CO_2 emission from fossil fuel use and cement production (Le Quéré *et al*., 2009). Eventually, improving the accuracy of NPP will lead to greater confidence in NEP estimation. In relation to ecosystem carbon budgets, the NPP-oriented analyses conducted in this study emphasize the importance of analyses on heterotrophic respiration (e.g., Davidson & Janssens, 2006; Bond-Lamberty & Thompson, 2010). Second, NPP is suitable for detecting the impacts of climate change and a rise in atmospheric CO_2 on terrestrial ecosystems. NEP is obtained as a small difference between large two gross fluxes (GPP and RE) and is strongly affected by irregular disturbances such as land-use change, making it difficult to detect long-term trends based on analyses of NEP. In contrast, NPP more clearly reflects environmental impacts (e.g., CO_2 fertilization effect and growing-period elongation) on the terrestrial biosphere (cf. Fig. 4). As shown in this study, a variety of data obtained through different methods are available for NPP, in terms of global terrestrial carbon budget, enabling us to examine long-term trends with greater credibility. Finally, NPP is closely related with ecosystem services such as provisioning of food, timber, fiber, and fuel wood including bio-energy crops and indicates climatic regulation on vegetation carbon fixation. Also, NPP supports biodiversity by providing genetic resources and soil formation via abandoned biomass. Several field experimental studies have suggested that fertile ecosystems tend to have higher biodiversity and are more resilient against external impacts (e.g., Tilman *et al*., 1997; Spehn *et al*., 2005). Therefore, improving our understanding of NPP will enable us to be better stewards (Chapin *et al*., 2009) of terrestrial ecosystems and the Earth system. This kind of historical meta-analysis of NPP_T and other comparable properties should be continued, as more and more estimates based on additional data and different methods are continually released.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. As in Figure 1 but plotted on a paper basis; that is, mean value is plotted if multiple estimates were provided in a single publication.

Table S1. Literature used in the historical meta-analysis.

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