Global Mapping of Terrestrial Primary Productivity and Light-Use Efficiency with a Process-Based Model

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Abstract. The carbon dynamics of terrestrial ecosystems was globally simulated with a mechanistic model, Sim-CYCLE, at a spatial resolution of $0.5^{\circ} \times 0.5^{\circ}$ in longitude and latitude. Gross photosynthetic production (GPP), net primary production (NPP), carbon storage, absorption of photosynthetically active radiation (APAR), and light-use efficiency (LUE) were addressed. Assuming an equilibrium state under the present environmental conditions, Sim-CYCLE estimated the annual global GPP and NPP as 124.7 and 60.4 Pg C yr⁻¹, respectively. Based on the estimated APAR of 191.3 \times 10²¹ J, the annual average biospheric LUEs for GPP and NPP were calculated as 0.652 and 0.315 g C MJ⁻¹, respectively. Global maps obtained by the model simulation illustrate the heterogeneity of ecosystem functions over the land surface, from tropical rain forests to polar deserts. There was a significant correlation between the estimated APAR and NPP ($r^2 = 0.62$, p < 0.0001); such model simulations and analyses should be effective for interdisciplinary research with remote sensing, in which a linear relationship between APAR and NPP is frequently assumed.

Keywords: carbon cycle, terrestrial ecosystems, mechanistic model, net primary production, photosynthetically active radiation

1. INTRODUCTION

Background

Terrestrial ecosystems play an important role in the global carbon cycle, as a huge reservoir and a regulator of atmospheric concentrations of carbon dioxide (CO₂) and methane (CH₄). This means that terrestrial ecosystems exert influences on climate systems through carbon exchange, as well as on energy and water exchanges (IPCC, 2001). This is the reason why the International Geosphere-Biosphere Program (IGBP) put focus on the global biogeochemical carbon cycle. However, because of the complexity and heterogeneity of terrestrial ecosystems, it is not easy to quantify the terrestrial carbon cycle with high accuracy and predict the impact of global environmental change. Investigations of the terrestrial carbon cycle are also required for carbon accounting under the Kyoto Protocol,

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in which the net carbon sequestration into forests due to management activities is taken into account. Thus, numerous efforts have been devoted to elucidating the global carbon cycle (in both land and ocean) through a variety of methods including field observation, remote sensing, and model simulation. The Global Carbon cycle and related MAPping based on Satellite imagery (GCMAPS) was launched to provide original data and a synthetic perspective related to the global carbon cycle. Recently, these efforts are being organized into the framework of the Global Carbon Project (Canadell *et al.*, 2000), a joint project of IGBP, World Climate Research Program (WCRP), and International Human Dimension Program (IHDP). The modelling approach is essential for carbon cycle studies at all levels from local to global, taking part in integrating empirical information, bridging different spatial scales, and making predictions.

Earlier model studies

The first global model of terrestrial ecosystems was developed in the early 1970s (Lieth, 1975), based on a large amount of observational data from the International Biological Programme (Whittaker, 1975). The model (called as Miami model) provided a good approximation of the global distribution of potential vegetation productivity. Esser (1987) extended the productivity model to simulate the entire carbon cycle, including biomass growth and soil carbon dynamics. Meanwhile, in Japan, Uchijima and Seino (1985) developed a micrometeorological model (called as Chikugo model) of vegetation productivity, in which net radiation is converted into dry-matter production. These empirical models were useful to retrieve the present state, but were not suitable for prediction under changing environments; for example, they could not provide a plausible estimation when atmospheric CO₂ increased significantly compared with the present level.

Accordingly, a mechanistic (i.e. process-based) model based on physiological regulation of processes was required for extrapolation to different environmental conditions. Melillo et al. (1993) published the first simulation results derived from a mechanistic model (Terrestrial Ecosystem Model, TEM); they estimated the response of terrestrial net primary productivity to elevated CO₂ and climate change. Subsequently, a multitude of mechanistic models have been developed, including BIOME-BGC by Running and Hunt (1993), Century by Parton et al. (1993), CASA by Potter et al. (1993), CARAIB by Warnant et al. (1994), SLAVE by Friedlingstein et al. (1995), FBM by Lüdeke et al. (1994), GTEC by Post et al. (1997), CEVSA by Cao and Woodward (1998), TsuBiMo by Alexandrov et al. (2002), and Sim-CYCLE by Ito and Oikawa (2002). These models adopt more or less the same approximation for ecosystem structure, i.e. the box-flow system, while they differ in parameterization of carbon flows (e.g. photosynthesis, respiration, allocation, litterfall, and decomposition), which are complex functions of various biological and environmental factors. Most models estimate major carbon flows, carbon storage in plants and soil, water- and light-use efficiency, and mean residence time of carbon. However, the difference in parameterization among the models resulted in a large difference in estimated carbon dynamics (Cramer $et\,al.$, 1999), indicating an uncertainty that remained to be dealt with. For example, Moldenhauer and Lüdeke (2002) discussed how to find the "best guess" based on several previous model estimations. Moreover, the interannual variability in productivity and net CO₂ exchange attracts attention from both observational and modelling researchers, who wish to investigate the responsiveness of the terrestrial carbon cycle to environmental perturbations (e.g. Potter $et\,al.$, 1999; Nemani $et\,al.$, 2003).

Objectives

Our objectives here are to (1) briefly describe a mechanistic model of the terrestrial carbon cycle, (2) demonstrate the results of a global simulation under present conditions, (3) compare the representative results with other studies, and (4) discuss the current problems and future directions. In relation to satellite remote sensing, we put special emphasis on light absorption and productivity estimated by the model. For brevity, detailed analyses of seasonal, latitudinal, and biome-specific aspects are beyond the scope of this paper.

2. METHODS

Model development

A process-based model, termed Simulation model of Carbon cYCle in Land Ecosystems (Sim-CYCLE) has been developed and used for analyzing atmospherebiosphere CO₂ exchange (Ito and Oikawa, 2000, 2002). Compared with other models, this model has a firm ecophysiological basis, which is attributable to both classic plant ecological theory (i.e. dry-matter production theory since Monsi and Saeki (1953)) and recent experimental findings. For example, stomatal regulation of gas exchange, a 2-component (construction and maintenance) respiration model, size-dependence of the plant respiration rate, acclimatization of respiration sensitivity to temperature, dependence of photosynthetic light-use efficiency on temperature and CO₂, and dependence of soil decomposition on temperature (parameterized by Lloyd and Taylor (1994)), are modern ecophysiological features incorporated in the model (see Ito and Oikawa (2002) for details). On the other hand, the ecosystem structure is captured in a rather simple manner (Fig. 1), for tractability in global simulations. Carbon storage in a terrestrial ecosystem is classified into 5 compartments: photosynthetic organs (leaves), aboveground non-photosynthetic organs (branches and stems), belowground non-photosynthetic organs (roots), dead biomass (litter), and mineral soil (humus). In temperate and tropical grasslands, additional plant compartments for C₄ species are introduced, because they differ largely from C₃ species in terms of photosynthetic capacity and environmental responsiveness. The annual mean temperature empirically determines the composition of C₃/C₄ species, so that C₄ species gradually become dominant as the temperature rises (Ito, 2003). For every time-step, 16 carbon flows (photosynthesis to decomposition) are calculated on the basis of the state

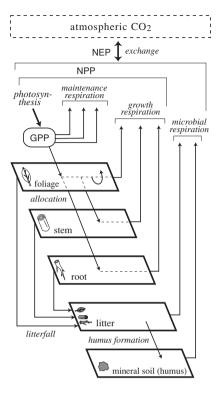


Fig. 1. Schematic diagram of the compartment model of terrestrial ecosystem carbon cycle used by Sim-CYCLE.

of carbon storage and environmental condition, and temporal variation in the carbon storage is simulated through iterative calculation. At this stage, impacts of natural and human disturbances (e.g. wildfire and land-use conversion) are not explicitly included.

Net primary productivity (NPP), one of the most representative indices of ecosystem functions, is estimated as the difference between gross photosynthetic production (GPP) and autotrophic plant respiration (AR):

$$NPP = GPP - AR. (1)$$

Thus, the NPP/GPP ratio becomes higher as respiratory carbon loss becomes lower, indicating the effectiveness of dry-matter production from photosynthate. GPP should be a complicated function of ecophysiological and environmental variables and is parameterized as follows (see Ito and Oikawa, 2002). (1) The light-photosynthetic rate relationship of a single leaf is approximated by a rectangular hyperbolic curve. (2) The light-saturated photosynthetic rate and

apparent light-use efficiency are formulated as functions of temperature, $\rm CO_2$ concentration, and soil water availability. And (3) the single-leaf photosynthetic rate is scaled up to canopy scale by integrating the leaf area index (LAI), taking light attenuation into account. Photosynthetically active radiation (wavelength 400–700 nm) absorbed by canopy (APAR) is obtained by

$$APAR = PAR_0(1 - \alpha)\{1 - \exp(-K \cdot LAI)\}$$
 (2)

where PAR₀ is canopy-top irradiance, α denotes canopy reflectance (0.14–0.20), and K is an attenuation coefficient that is a function of biome type and solar angle. Light-use efficiency of photosynthetic production (LUE, in g C MJ⁻¹) is defined as:

$$LUE = GPP'/APAR'$$
 (3)

where GPP' and APAR' are cumulative GPP and APAR for a given period (e.g. 1 yr), respectively. LUE for NPP would be defined in a similar manner.

Autotrophic respiration (AR) is composed of 6 independent flows: construction and maintenance respirations from leaf, stem, and root. The maintenance respiration rate is a function of the amount of standing biomass and the specific respiration rate, which is sensitive to the temperature and activity of the organ. In general, the specific respiration rate approximately doubles as the temperature rises by 10°C, and active organs (leaves, sap wood, and fine roots) have higher specific rates than inactive organs (heart wood and tap roots). In the model, the sensitivity coefficient of the temperature response (Q_{10}) is parameterized as functions of temperature to represent acclimatization, and specific respiration rates of stem and root are parameterized as a function of the amount of standing biomass, in order to represent size-dependence. Construction respiration does not directly respond to environmental conditions but is proportional to the rate of biomass growth; thus, the construction respiration rate indirectly varies with environmental conditions, in parallel with the photosynthetic carbon assimilation rate.

Allocations of photosynthate, litterfall, and soil processes are also simulated in rather simple manners. Decomposition of soil organic matter (litter and humus) by microbes is strongly dependent on temperature and water content. Phenological (i.e. seasonal) change in allocation and litterfall is difficult to express in a mechanistic manner, and are thus parameterized in a rather empirical manner. The onset of the growing period is determined from the cumulative temperature above a critical temperature (5°C); for example, 300°C·day is required for budbreak in temperate deciduous broad-leaved forest. In grasslands, not only temperature but also soil water content (>10% water holding capacity) restricts the length of the growing period. Termination of the growing period is determined by occurrence of cooling below the critical temperature (the photoperiod is not considered).

Data and simulation design

A global simulation is performed with a spatial resolution of $0.5^{\circ} \times 0.5^{\circ}$ in longitude and latitude. The biome distribution is derived from an actual vegetation map of Olson *et al.* (1983); natural vegetation is classified into 28 types, and there are 4 types of cropland (Table 1). The carbon cycle model is applied to each of the grid points with vegetation cover (58772 points, 132.3×10^6 km²). The 28 natural vegetation types include representative biomes, such as tropical rain forest, savanna, temperate deciduous broad-leaved forest, steppe, boreal needle-

Table 1. Category and area of 32 biomes. Estimated net primary production (NPP) by Sim-CYCLE and Cramer *et al.* (1999) are compared (for overlapping areas).

	Category (revised Olson et al. (1983))	Area 10^6 km^2	This study		Cramer et al. (1999)	
			Total*	Density**	Total*	Density**
1	Tropical and subtropical evergreen forest	10.5	11.2	1072	9.9	950
2	Tropical montane forest	1.2	1.1	910	1.1	890
3	Tropical and subtropical dry forest	4.7	3.6	767	2.7	572
4	Mid-latitude mixed woods	3.5	2.1	598	1.9	547
5	Mid-latitude broad-leaved forest	1.5	0.7	461	0.8	529
6	Semiarid wood or low forest	0.9	0.2	209	0.3	368
7	Coniferous forest	3.5	1.8	503	1.5	421
8	Southern taiga	1.6	0.4	262	0.6	367
9	Main boreal taiga (evergreen)	3.4	1.4	409	1.2	347
10	Main boreal taiga (deciduous)	2.1	0.8	381	0.7	325
11	Northern taiga (evergreen)	2.7	0.9	324	0.7	253
12	Northern taiga (deciduous)	1.6	0.5	325	0.4	231
13	Second growth woods	5.2	2.6	511	3.2	625
14	Second growth fields	4.1	1.7	408	2.5	607
15	Succulent and thorn woods	4.0	2.1	534	1.5	366
16	Tropical savanna, woodland	6.7	4.5	665	4.4	654
17	Mediterranean-type dry woods	3.6	1.1	292	0.9	258
18	Heath and moorland	0.1	0.0	245	0.1	346
19	Warm or hot shrub and grassland	17.3	5.8	334	6.6	378
20	Tibetan meadow, Siberian highland	0.8	0.1	160	0.2	184
21	Tundra	9.9	1.9	194	1.4	142
22	Wooded tundra	1.7	0.4	229	0.3	199
23	Warm or hot wetlands	1.6	0.9	567	1.1	692
24	Cool bog and mire	1.0	0.3	277	0.3	350
25	Shore and hinterlands	1.0	0.3	256	0.3	298
26	Cool semi-desert scrub	2.0	0.4	193	0.4	216
27	Non-polar desert	11.1	1.4	125	1.1	101
28	Non-polar sand desert	5.2	0.6	112	0.5	93
29	Paddyland	2.0	1.2	609	1.2	627
30	Cool croplands	3.0	1.1	387	1.4	468
31	Warm croplands	13.2	5.3	399	6.4	485
32	Irrigated	1.6	0.4	237	0.4	255
	Total	132.3	56.7		56.0	

^{*}Total in Pg C yr^{-1} , **Density in g C m^{-2} yr^{-1} .

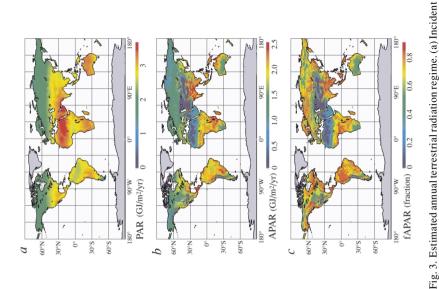
leaved forest, desert, and tundra. They are characterized by differences in ecophysiological parameters and phenological patterns (evergreen, winter deciduous, and dry deciduous). Altitude and soil conditions (water holding capacity and rooting depth) are derived from ETOPO5 and a global soil dataset (Webb *et al.*, 1993), respectively. Climatic condition is obtained from a global dataset of the U.S. National Centers for Environmental Prediction and the National Center for Atmospheric Research (NCEP/NCAR; Kistler *et al.*, 2001) in terms of cloudiness, temperatures (air, surface, and subsurface), precipitation, specific humidity, and wind. Since the original NCEP/NCAR data were produced for a T62 Gaussian grid (about $1.9^{\circ} \times 1.875^{\circ}$), each climatic field is interpolated into a $0.5^{\circ} \times 0.5^{\circ}$ grid, taking the altitudinal temperature lapse rate into account. Using these climatic input variables, a sub-module of the water and energy budget estimates vapour pressure deficit, net radiation, evapotranspiration, runoff, and soil water content (see Ito and Oikawa, 2002).

In the present study, an equilibrium state of carbon dynamics was obtained by iterative calculation assuming a stationary environmental condition: a long-term mean climate condition (from 1961 to 1998) and an atmospheric ${\rm CO_2}$ concentration of 350 ppmv. The simulation time-step was 1 month. Starting from an initial condition (with a tiny carbon storage), the iteration continued until satisfying the criterion of stable carbon dynamics: annual net carbon exchange with the atmosphere should be smaller than 0.1 g C m⁻²yr⁻¹, as expected in a mature ecosystem.

3. RESULTS

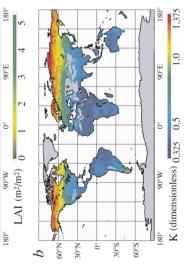
Global annual carbon dynamics

Sim-CYCLE calculated that the annual influx of PAR over the vegetation area would be 352.2×10^{21} J. At the equilibrium state, Sim-CYCLE estimated that the global total leaf area would be 419.4×10^6 km², which absorbed 191.3×10^{21} J of PAR per year (i.e. 54% of influx). The average area-weighted LAI was estimated as 3.17 m² m⁻². The annual gross photosynthetic production (GPP) and net primary production (NPP) were estimated as 124.7 and 60.4 Pg C (1 Pg C = 10¹⁵ g C), respectively. Thus, the annual mean biospheric LUE (see Eq. (3)) of CO₂ assimilation (GPP) was calculated as 0.652 g C MJ⁻¹; similarly, the annual mean biospheric LUE of dry-matter production (NPP) was obtained as 0.315 g C MJ⁻¹. The estimated GPP and NPP are comparable with results from former studies; for example, the global annual NPP has been estimated as 53.2 Pg C by Melillo et al. (1993), 56.4 Pg C by Field et al. (1998), and 62.6 Pg C by Roy et al. (2001). The estimated global APAR was higher than that of Ruimy et al. (1999), 111 ± 17 (SD) $\times 10^{21}$ J, simply because those authors performed the calculation over a smaller land area (35304 points, compared with 58772 points in this study). Eventually, the estimated light-use efficiency of NPP falls within the range among 12 models in Ruimy et al. (1999), i.e. 0.427 ± 0.126 (SD) g C MJ^{-1} .





photosynthetically active radiation (PAR), (b) canopy-absorbed PAR (APAR), and (c) fraction of canopy absorption (fAPAR).



The total carbon storage in the terrestrial biosphere was estimated to be 1856 Pg C, of which 504 Pg C was stored in plant biomass and 1352 Pg C in soil organic matter. The estimated soil carbon storage is sufficiently close to the empirical estimation of 1395.3 Pg C, by Post *et al.* (1982). Based on annual litter production rates (26.4 Pg C from foliage, 11.7 Pg C from stems, and 20.8 Pg C from roots), the mean residence time of plant biomass was calculated: 1.0 yr for leaves, 33.8 yr for stems, and 3.9 yr for roots. Litter and mineral soil indicated disparate mean residence times: 1.6 yr for litter and 36.5 yr for mineral soil. Additionally, based on the litter production rates, NPP was separated into aboveground (38.1 Pg C) and underground (20.8 Pg C) components.

 C_4 species, which were assumed to occur only in grasslands, were expected to play an important role in the global carbon cycle, although their biomass was tiny (15.6 Pg C) compared with C_3 (woody) species (488.5 Pg C). The annual CO_2 fixation through the C_4 photosynthetic pathway was estimated as 35.1 Pg C (28.1% of the land total); this result is comparable with another recent estimation, 35.3 Pg C, by Still *et al.* (2003). This result implies that the mean residence time of carbon in C_4 species should be remarkably shorter than in C_3 species.

Patterns

Figure 2 shows the estimated distributions of LAI and the light attenuation coefficient (K in Eq. (2)). We found an apparent contrast in LAI between arid and humid regions, and a gradient in K with latitude (note that K depends on solar angle). For example, tropical rain forests have higher LAI (e.g. 5) and moderate K (e.g. 0.5), whereas arctic tundra ecosystems have lower LAI (e.g. 1) and higher K (e.g. 0.8). Tropical savannah, dominated by C_4 grass species, shows moderate LAI (e.g. 3) and lower K (e.g. 0.4). Because of these differences in canopy architecture, there occurred an apparent difference in solar energy absorption by plant canopy. Figure 3 shows the estimated distribution of incident PAR, canopyabsorbed PAR (APAR), and the fraction of absorbed PAR (fAPAR). Obviously, arid regions at lower latitudes receive higher incident PAR, although tropical rain forests receive only moderate incident PAR because of shading by clouds. APAR was higher in tropical and subtropical forests, while grasslands and deserts at lower latitudes absorbed only a small fraction of incident PAR. Thus, not only is incident PAR important in determining APAR, but so are LAI and K. Finally, high fAPAR was found in both tropical humid regions (with high LAI) and northern evergreen forests (with high K). The overall pattern of fAPAR seems consistent with the satellite-based estimation by Sellers et al. (1994).

Estimated GPP and NPP show a similar global distribution (Fig. 4): from highest in tropical rain forests (NPP: around 1000 g C m⁻²yr⁻¹) to lowest in subtropical and northern deserts (NPP: around 10 g C m⁻²yr⁻¹). Several intensively cultivated areas (middle North America, monsoon Asia, and western and central Europe) show moderate productivities. The highest NPP/GPP ratio (Fig. 5) occurred in boreal forests, where the respiration rate is restricted by low temperature. Grassland ecosystems showed lower NPP/GPP ratios; this is largely

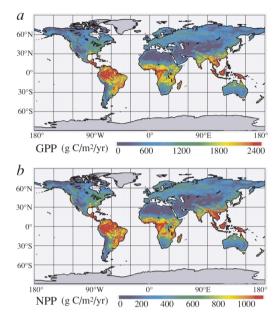


Fig. 4. Estimated annual terrestrial productivity. (a) Gross photosynthetic production (GPP) and (b) net primary production (NPP).

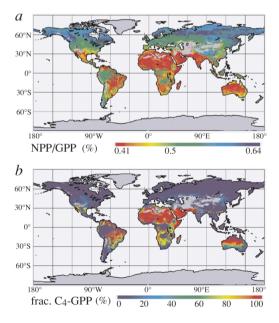


Fig. 5. Estimated features related to vegetation production. (a) GPP/NPP ratio and (b) fractional contribution by C_4 species to GPP.

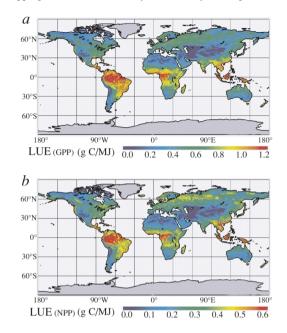


Fig. 6. Estimated annual mean light-use efficiency (LUE), for (a) GPP and (b) NPP.

attributable to their high respiration from large root biomass. Figure 5 also shows the contribution by C_4 species to ecosystem NPP; as expected from their geographical distribution, C_4 species made a higher functional contribution in tropical and subtropical grasslands.

On the basis of the estimated productivity and PAR absorption, light-use efficiency was calculated for GPP and NPP (Fig. 6). Global patterns of the 2 LUEs seem similar to each other, in that tropical rain forests show higher LUE (e.g. 0.8 g C MJ⁻¹ for GPP) and subtropical and temperate deserts show lower LUE. Temperate and boreal forests show comparable LUE (about 0.6 g C MJ⁻¹ for GPP), irrespective of phenology and woody types. As shown by Fig. 7, we found a significant correlation between the estimated productivity and absorbed PAR across the terrestrial grid points: $r^2 = 0.67$ (p < 0.0001) for the GPP-APAR relationship, and $r^2 = 0.62$ (p < 0.0001) for the NPP-APAR relationship. It seems that there is no obvious light-saturation in canopy photosynthesis at the global scale. However, it is also apparent that there is a wide range of scattering in the APAR-NPP relationship, stemming from differences in environmental conditions (e.g. temperature and water availability) and plant properties (e.g. LAI and nonassimilative biomass). In spite of the wide range of disparity in high APAR areas, these relationships are sufficiently consistent with former studies (e.g. Ruimy et al., 1999; Turner et al., 2003), supporting the validity of the present model analyses.

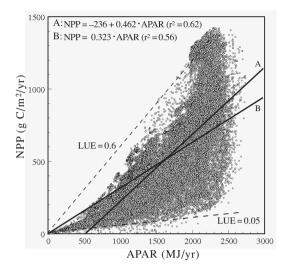


Fig. 7. Correlation between absorbed photosynthetically active radiation (APAR) and net primary production (NPP) across the global terrestrial grid points.

4. DISCUSSION AND CONCLUSION

Global carbon cycle and terrestrial ecosystems

In this study, a mechanistic model of terrestrial carbon cycle was used for global mapping of carbon flows and pools, placing emphasis on PAR absorption and light-use efficiency. The estimated gross photosynthetic rate (124.7 Pg C yr⁻¹) and total carbon storage (1856 Pg C) confirm that the terrestrial biosphere should play an important role in the global carbon cycle. Although carbon in stem and humus is relatively passive and has a moderate mean residence time (decades or centuries), biogeochemical carbon cycling in terrestrial ecosystem is remarkably dynamic and can be reactive to global environmental change. The present simulation suggests that the terrestrial carbon cycle may be distributed heterogeneously over the land surface (see Figs. 2 to 6); this is one of the peculiar aspects of terrestrial ecosystems, compared with those of the ocean and atmosphere.

Because the terrestrial carbon cycle is driven by solar energy through photosynthetic assimilation of atmospheric CO₂, light-use efficiency (LUE) is a very important index for ecological and micrometeorological studies. LUE is also important for remote sensing studies, because most satellite-based estimations of vegetation productivity rely on the relationship between APAR and NPP (Kumar and Monteith, 1981) (see Eq. (3)). The present study provided a model-based estimation of LUE (Fig. 6), considering physiological and environmental factors. On the other hand, remote sensing data would make modelling studies more realistic, in terms of heterogeneous and non-stable features of the land surface.

Comparison with other estimations

In this section, a comparison is made for NPP between the Sim-CYCLE estimation and another model estimation by Cramer et al. (1999), which is an average of 16 models that participated in the Potsdam Model Intercomparison. Because observational data of NPP (and other carbon cycle features) are still fragmentary (Zheng et al., 2003), intercomparison among models may allow us a more robust validation, especially on a global scale. Additionally, model intercomparison is effective for clarifying differences concerning the assumptions, parameterizations, and structures between models (Ryan et al., 1996). Consequently, the global grid-by-grid comparison (for the 49878 overlapping points) showed that the NPP estimated by Sim-CYCLE strongly agrees with the 16-model average by Cramer *et al.* (1999): $r^2 = 0.61$ (p < 0.0001, Table 1). The global annual NPP by Sim-CYCLE (56.7 Pg C for the overlapping area) is adequately close to the 16-model average (56.0 Pg C). However, as shown in Table 1, Sim-CYCLE gave higher NPP in tropical rain forests, subtropical dry forests, and succulent woodlands, but lower NPP in semiarid woodlands, second growth fields, and warm grasslands.

Problems and future studies

There remain several practical problems in the global mapping of the terrestrial carbon cycle with a mechanistic model. (1) The spatial resolution, 0.5° $\times 0.5^{\circ}$, may be too coarse to capture the heterogeneity of the land surface induced by topography, geology, and disturbances (such as fires and windthrows). For example, in tropical savannahs and inland boreal forests, frequent wildfires lead to heterogeneities of species composition, age distribution, carbon storage, and net CO₂ exchange. To ameliorate the uncertainty due to sub-grid scale heterogeneities, models are expected to operate at a higher resolution, and the heterogeneity factors should be parameterized on the basis of observational data. (2) The estimated LAI and K necessary to obtain APAR have not been fully validated with observational data. Although several studies have derived global maps of LAI from satellite data (e.g., Knyazikhin et al., 1998), it is still premature to use these LAI data for model validation. (3) Model simulation at flux measurement sites would provide clear validation of the model with respect to net CO₂ exchange at the ecosystem level. Analyses of seasonal and interannual variability in relation to environmental variability may clarify whether model assumptions and parameterizations are appropriate or not. In our ongoing studies, the model is actually applied to several representative flux measurement sites. (4) We emphasize again that the model-based mapping of NPP, APAR, and LUE can be directly compared with satellite-based mapping. Such interdisciplinary research would be effective and important for elucidating the global carbon cycle, which includes diverse processes and spans various temporal and spatial scales. Collaboration of modelling and remote sensing efforts is required to make accurate projections of global change in the future, on the basis of our present knowledge.

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