Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency

A. RUIMY 1, L. KERGOAT 2,3, A. BONDEAU 4 and THE PARTICIPANTS OF THE POTS DAM NPP MODEL INTERCOMPARISON*

1Laboratoire d’Ecophysologie Végétale, Bâtiment 362, Université Paris-Sud, F-91405 Orsay Cedex, France, 2Centre d’Études Spatiales de la Biosphère, bpi 2805, 18, Av Edouard Belin, F-31055 Toulouse Cedex, France, 3Present address: Laboratoire d’Ecologie Terrestre, 13, Av Cézine, BP 4403, F-31054 Toulouse Cedex 4, France, 4Potsdam Institut für Klimafolgenforschung e.V. (PIK), Postfach 60 12 03, Telegrafenberg, D-14412 Potsdam, Germany


³Previous name: A. Fischer.

Abstract

Twelve global net primary productivity (NPP) models were compared: BIOME3, CASA, CARAIB, FBM, GLO-PEM, HYBRID, KGBM, PLAI, SDBM, SIB2, SILVAN and TURC. These models all use solar radiation as an input, and compute either absorbed solar radiation directly, or the amount of leaves used to absorb solar radiation, represented by the leaf area index (LAI). For all models, we obtained or estimated photosynthetically active radiation absorbed by the canopy (APAR). We then computed the light use efficiency for NPP (LUE) on an annual basis as the ratio of NPP to APAR. We analysed the relative importance for NPP of APAR and LUE. The analyses consider the global values of these factors, their spatial patterns represented by latitudinal variations, and the overall grid cell by grid cell variability. Spatial variability in NPP within a model proved to be determined by APAR, and differences among models by LUE. There was a compensation between APAR and LUE, so that global NPP values fell within the range of ‘generally accepted values’. Overall, APAR was lower for satellite driven models than for the other models. Most computed values of LUE were within the range of published values, except for one model.

Keywords: NPP, model, global, intercomparison, light use efficiency

Introduction

Terrestrial net primary productivity (NPP) is the difference between photosynthesis, or gross primary productivity (GPP), and autotrophic respiration (R_A), integrated over a year. NPP is an important variable in studies of the global carbon cycle, as it determines the rate of absorption of atmospheric carbon by land vegetation.

Recently, several models of terrestrial NPP have been developed, reflecting increasing concern about anthropogenic perturbations to the global carbon cycle and global climate. In contrast to oceanic NPP, global terrestrial NPP estimates have not varied much historically, being usually in the 40–80Pg C year⁻¹ range (Cramer et al. 1999). However, models that agree on the value of certain outputs (e.g. annual NPP) may disagree on the underlying processes (e.g. differences in rates of
photosynthesis vs. plant respiration, seasonal differences in NPP, differences in light absorption vs. light conversion into dry matter, etc.). This is a cause for concern when the models are applied to scenarios of the future, such as increased atmospheric CO₂ concentration. In addition to current estimates of global NPP, this model intercomparison (Cramer et al. 1999) provides clues to the understanding of the processes that lead to the net absorption of CO₂ by plants, i.e. how plants capture and transform environmental resources to produce dry matter.

In this study, we focus on solar radiation, an essential resource for NPP because it is the source of energy that drives the process of photosynthesis. Atmospheric CO₂ is incorporated into dry matter via the consecutive processes of photosynthesis and biosynthesis, each step associated with a yield (or efficiency) of transformation of the solar energy. Our approach for the model intercomparison uses the concept of Monteith (1972, 1977) as a diagnostic tool. The underlying philosophy is that geometrical factors leading to absorption of solar radiation (e.g. leaf area index, leaf orientation, leaf optical properties) are relatively independent from biological factors resulting in storing carbon in dry matter by transformation of the absorbed solar energy. Decomposing NPP estimates into geometrical and biological factors integrates most individual processes leading to NPP into a limited number of factors. It is therefore a powerful tool that permits more thorough analyses of models than does a simple comparison of simulated NPP.

We use an *a posteriori* decomposition of model outputs of NPP into factors for the use of solar radiation. Fifteen of 17 global models in the intercomparison use solar radiation as a driver of plant productivity (Cramer et al. 1999). We compare the 12 global models that: (1) use solar radiation as an input, and (2) either derive directly the fraction of light absorbed by the canopy, or provide the basis to calculate it. We present a brief description of light use in the models and the analyses that were performed. The objectives of this study are, first, to determine which of the geometrical or biological factors is most important in generating differences in NPP among models at different spatial scales, and second, to begin assessing what model characteristics generate the differences in these factors for light use.

**Methods**

**Models**

In this study, we consider 12 models (for References, cf. Cramer et al. 1999): BIOME3, CASA, CARAIB, FBM, GLO-PEM, HYBRID, KGBM, PLAI, SDBM, SIB2, SILVAN and TURC. Other models were involved in the Potsdam Model Intercomparison workshop but are not included here, because they either did not use solar radiation as an input, or were not able to provide the basis to compute absorbed solar radiation. The models can be classified into two broad categories, according to the way they model the absorption of solar radiation and its conversion into dry matter

*Production Efficiency Models (PEMs)* (CASA, GLO-PEM, SDBM and TURC). PEMs are based on the Kumar & Monteith (1981) approach. In these models, the fraction of solar radiation absorbed by terrestrial vegetation is calculated from remote sensing data, such as the Normalized Difference Vegetation Index (NDVI) recorded by NOAA-AVHRR satellites. The conversion of absorbed radiation into dry matter can be computed from a variety of approaches: a constant ‘conversion efficiency’, or the product of an optimum value by other factors representing environmental stresses. The PEM concept may be applied to the computation of GPP, in which case autotrophic respiration is computed independently (in GLO-PEM and TURC). PEMs are sometimes called ‘diagnostic models’ because they use remote sensing data as inputs.

*Canopy Photosynthesis Models (CPMs)* (BIOME3, CARAIB, FBM, HYBRID, KGBM, PLAI, SIB2 and SILVAN). CPMs evolved from ecosystem or crop models that were originally developed for use at a local scale. In these models, GPP is first computed at the leaf level with a more or less mechanistic model coupling the exchanges of CO₂ and water, then integrated through the canopy. The integration is usually done by coupling the simulations of seasonal canopy development (seasonal variations of leaf area index or LAI) and biochemical fluxes (CO₂ and water exchanges). All the CPMs in this study except SIB2 use an empirical model, a simple Beer–Lambert law, to integrate GPP through the canopy. SIB2 uses remotely sensed FPAR to scale leaf photosynthesis, itself computed mechanistically, to the canopy, much like in PEMs. CPMs are sometimes called ‘process models’ because they usually explicitly compute the different processes of plant productivity: photosynthesis, respiration, allocation of assimilates, phenology, mortality. They are also referred to as ‘prognostic models’ when they are used to make predictions for the future, in the absence of remote sensing measurements.

Models are often classified in categories similar to these (Cramer et al. 1999). In this study, we assess whether the categories reflect actual differences in model behaviour, and in particular whether the different types of models, PEMs and CPMs, are different with respect to their factors for light use. For more information on the structure and
assumptions of the models, we refer to Cramer et al. (1999), as well as the original articles describing individual models.

Analyzes

For each model, we obtained or estimated the fraction of light absorbed by plant canopies. We first converted incident global radiation provided by the standard data sets (Cramer et al. 1999) into photosynthetically active radiation (PAR), using a constant ratio of 0.48 MJ (PAR) MJ$^{-1}$ (global radiation) (McCree 1972). In fact, the models may use a different ratio of PAR to global radiation, or even time- or space-varying ratios. BIOME3, CARAIB, FBM, HYBRID, KGBM, PLAI and SILVAN do not explicitly calculate light absorption at the canopy level, but compute a leaf area index (LAI). For these models we estimated the total fraction of incident PAR absorbed by the canopy with a Beer–Lambert law, similar to the scheme used in most CPMs in this study to integrate leaf photosynthesis to the canopy:

$$\text{FPAR} = 0.95(1 - \exp(-k'\text{LAI}))$$  \hspace{1em} (1)

where FPAR is the fraction of incident PAR absorbed by the canopy (dimensionless), $k$ is the light extinction coefficient, and LAI is leaf area per ground area (m$^2$ m$^{-2}$).

We used a constant value of 0.5 for $k$, typical for both herbaceous crops (Varlet-Grancher 1980) and for coniferous forests (Jarvis & Leverenz 1983). In fact, $k$ can be substantially different, in particular for broadleaf forests (Jarvis & Leverenz 1983), and actual values of $k$ used in models may vary spatially and temporally. For the seven models above, plus CASA, GLO-PEM, SDBM, SILVAN and TURC which provided FPAR on a monthly basis, we then calculated the annual APAR:

$$\text{APAR} = \text{FPAR} \cdot \text{PAR}$$  \hspace{1em} (2)

where PAR is incoming photosynthetically active radiation (MJ year$^{-1}$ m$^{-2}$), and APAR is annual absorbed photosynthetically active radiation (MJ year$^{-1}$ m$^{-2}$).

All models provided annual and monthly NPP. For the 11 models above, plus SIB2 which provided annual APAR, we then decomposed a posteriori NPP into absorbed PAR, and conversion of absorbed PAR into dry matter:

$$\text{NPP} = (\text{NPP}/\text{APAR}) \cdot \text{APAR} = \text{LUE} \cdot \text{APAR}$$  \hspace{1em} (3)

where NPP is annual net primary productivity (g C year$^{-1}$ m$^{-2}$), and LUE is light use efficiency of NPP (g C MJ$^{-1}$).

**Fig. 1** Grid cell level regression of net primary productivity (NPP) (kg C year$^{-1}$ m$^{-2}$) against absorbed photosynthetically active radiation (APAR) (GJ year$^{-1}$ m$^{-2}$). Linear correlation coefficient ($r^2$), slope (a) and intercept (b) are indicated for each model, $n = 35304$. © 1999 Blackwell Science Ltd., Global Change Biology, 5 (Suppl. 1), 56–64
The relationships were analysed between NPP and its components, APAR and LUE, at three spatial levels: the grid cell level, the zonal level, and the global level. We defined a common area of 35,304 grid cells to ensure a positive annual NPP and strictly positive APAR for all the 0.5° × 0.5° grid cells. This mask mainly discards desert areas. For the grid cell level analyses, we plotted within each model the values of NPP vs. APAR and LUE for all grid cells of the common area. These plots allow analysis of intramodel relationships, or the relationships between NPP and its components within models. At the global scale, we first integrated the considered variables over the entire common area, then plotted global values of NPP vs. APAR and LUE for the 12 models included in this study. These plots allow analysis of intermodel relationships, or the relationships between NPP and its components among models.

We performed linear regressions on the global and grid cell level plots. Correlations were usually measured by \( r^2 \), but \( r \) was preferred when the sign of the correlation is important. At the zonal scale, we first integrated the variables considered over 0.5° latitudinal bands of the common area, then plotted the zonal profiles of NPP, APAR and LUE. These plots illustrate the general spatial pattern of NPP and its components for each model.

**Results**

**Grid cell level analyses**

Correlations between annual NPP and annual APAR at the grid cell level are generally high (Fig. 1). For instance, APAR explains over 90% of NPP variance for two models by \( r^2 \), but \( r \) was preferred when the sign of the correlation is important. At the zonal scale, we first integrated the variables considered over 0.5° latitudinal bands of the common area, then plotted the zonal profiles of NPP, APAR and LUE. These plots illustrate the general spatial pattern of NPP and its components for each model.

These regressions are not performed on strictly independent variables, as they should be. Indeed, because the objects of the analyses are models, not data, each model uses in a more or less complex fashion the ‘independent’ variable APAR to compute the ‘dependent’ variable NPP. More importantly, the ‘independent’ variable LUE is directly calculated as the ratio of the ‘dependent’ variable NPP, and APAR. NPP and LUE are thus auto-correlated. In this study, however, we assess which of its components, APAR or LUE, is more important in determining NPP at different spatial scales, and not to establish relationships between independent variables.

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1 The masks used in related NPP intercomparison papers are different because different subset of models are analysed. As a consequence the global values of NPP reported here can be different from the global means reported for the area over which the models were run, or the areas considered in the related papers in this issue.

2 These regressions are not performed on strictly independent variables, as they should be. Indeed, because the objects of the analyses are models, not data, each model uses in a more or less complex fashion the ‘independent’ variable APAR to compute the ‘dependent’ variable NPP. More importantly, the ‘independent’ variable LUE is directly calculated as the ratio of the ‘dependent’ variable NPP, and APAR. NPP and LUE are thus auto-correlated. In this study, however, we assess which of its components, APAR or LUE, is more important in determining NPP at different spatial scales, and not to establish relationships between independent variables.
(CASA and TURC), and over 70% of NPP variance for six other models (BIOME3, CARAIB, HYBRID, KGBM, SILVAN and SDBM). The intercepts obtained by regression are close to zero. Correlations between annual NPP and LUE are weaker (Fig. 2), and the intercepts usually depart from zero (e.g. in CASA). Thus, the variations of NPP within models depend primarily on variations of APAR, and effects of LUE are second-order effects.

SIB2 is an exception, with a higher correlation of NPP with LUE than with APAR. Possible reasons for the different behaviour of SIB2 are:

1. SIB2 is, in contrast to other CPMs, where climate is a model input, coupled to a General Circulation Model which simulates its own climate. NDVI-derived FPAR, on the other hand, is a model input, so that high PAR capture does not necessarily correspond to favourable climate;

2. leaf photosynthesis is computed mechanistically and at very short time-steps, while APAR is only a correction factor applied monthly to scale leaf photosynthesis over the entire canopy. GLO-PEM is also an exception, with low correlations with either NPP or APAR. It is the only model that totally relies on remotely sensed data to derive most climate inputs and model parameters. These algorithms apparently result in a wide range of LUE, and are also possibly rejected for some ‘noisy’ grid cells, thus giving the zero NPP/non zero APAR grid cells that lower the NPP/APAR correlation.

The high correlations between NPP and APAR and the near-zero intercept for most models, PEMs and CPMs alike, means that these models can be, at first order, approximated by a PEM structure, with a constant, model-specific light use efficiency (the slopes of the regression range from 0.39 to 0.52 for the seven highest correlations). Thus, the distinction between PEMs and CPMs may not be very important. Some of the reasons why CPMs behave like PEMs include:

1. While the first generation of PEMs may have been less mechanistic than CPMs, the refinements introduced to the latest generation of PEMs, such as stress factors reducing LUE, bring them closer to CPMs;

2. The use of a linear light–response curve (in PEMs) vs. a saturating curve (in CPMs) may not be a big difference at the temporal and spatial scales considered, as integration in space and time tends to linearise light response curves (Ruimy et al. 1995);

3. Some CPMs use simplifications (‘optimized Farquhar models’ in BIOME3 and SILVAN for example) that...

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**Fig. 3** Global level regressions. (a) Global NPP (Pg C year⁻¹) against mean global APAR (10¹⁸ J year⁻¹); (b) Global NPP (Pg C year⁻¹) against mean LUE (g C MJ⁻¹); (c) Global LUE (g C MJ⁻¹) against mean global APAR (10¹⁸ J year⁻¹). Linear correlation coefficients (r) are indicated. The models are: BIOME3 (b), CARAIB (cr), CASA (cs), FBM (f), GLO-PEM (g), HYBRID (h), KGBM (k), PLAI (p), SDBM (sd), SIB2 (sb), SILVAN (sl), and TURC (t).
Table 1: Global values of NPP, APAR and LUE for the models included in this study. The numbers outside parentheses are surface-weighted average of fluxes and factors computed from the 33,204 grid cells of the common area, the numbers in parenthesis are NPP and APAR for the total area.

<table>
<thead>
<tr>
<th>Model</th>
<th>NPP (Pg C)</th>
<th>APAR (10^18 J)</th>
<th>LUE (g C MJ^-1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIOME3</td>
<td>42.6 (59)</td>
<td>132 (185)</td>
<td>0.307</td>
</tr>
<tr>
<td>CARAIB</td>
<td>52.5 (65)</td>
<td>105 (133)</td>
<td>0.500</td>
</tr>
<tr>
<td>CASA</td>
<td>38.5 (49)</td>
<td>88 (115)</td>
<td>0.410</td>
</tr>
<tr>
<td>FBM</td>
<td>41.5 (50)</td>
<td>128 (157)</td>
<td>0.327</td>
</tr>
<tr>
<td>GLO-PEM</td>
<td>53.2 (66)</td>
<td>86 (113)</td>
<td>0.671</td>
</tr>
<tr>
<td>HYBRID</td>
<td>31.6 (40)</td>
<td>108 (149)</td>
<td>0.302</td>
</tr>
<tr>
<td>KGBM</td>
<td>51.0 (63)</td>
<td>104 (132)</td>
<td>0.506</td>
</tr>
<tr>
<td>PLAI</td>
<td>39.6 (51)</td>
<td>137 (180)</td>
<td>0.302</td>
</tr>
<tr>
<td>SDBM</td>
<td>47.4 (62)</td>
<td>100 (144)</td>
<td>0.456</td>
</tr>
<tr>
<td>SIB2</td>
<td>41.4 (57)</td>
<td>128 (183)</td>
<td>0.319</td>
</tr>
<tr>
<td>SILVAN</td>
<td>47.7 (64)</td>
<td>116 (155)</td>
<td>0.410</td>
</tr>
<tr>
<td>TURC</td>
<td>58.0 (80)</td>
<td>98 (135)</td>
<td>0.609</td>
</tr>
<tr>
<td>mean</td>
<td>45.5 (59)</td>
<td>111 (148)</td>
<td>0.427</td>
</tr>
<tr>
<td>std</td>
<td>7.5</td>
<td>17.1</td>
<td>0.126</td>
</tr>
<tr>
<td>CV</td>
<td>0.17</td>
<td>0.15</td>
<td>0.29</td>
</tr>
</tbody>
</table>

reduce GPP to a product of a light-response curve by other factors, much like in PEMs;
4 Even though photosynthesis and autotrophic respiration are sensitive to different environmental variables (McCree 1974), at first order, respiration is proportional to GPP.

Global level analyses

Given the importance of APAR on NPP estimation at the grid cell level, it is interesting to see how this strong relationship translates into global values. In contrast to grid cell level relationships, differences among the models in global NPP estimates do not correspond to differences in global APAR estimates (Fig. 3a). Moreover, the weak trend observed is a negative correlation ($r = -0.42$): the more a model absorbs PAR, the lower its NPP estimate. Instead, differences among models in global NPP are highly correlated with LUE ($r = 0.86$) (Fig. 3b). This indicates that differences in NPP among models are due to differences in LUE.

The differences in LUE are larger that the differences in NPP, and LUE effects are partially compensated by differences in APAR: in fact, there is a surprising negative correlation between the global values of APAR and LUE (Fig. 3c). The relationship is close to a hyperbola of the equation $APAR \times LUE = \text{constant}$, indicating that there may be either explicit or unconscious adjustment of parameters within models, with the consequence that global results are within a commonly accepted range. The fact that these models could be calibrated puts a damper on the confidence that we may have in global models of NPP, confidence resulting from the fact that global estimates have changed little since Lieth (1975) estimated global NPP to be around 60 Pg C year$^{-1}$. On the other hand, many models are conceived as tools for formalizing the complex relationships between NPP and forcing factors, rather than estimating the absolute value of NPP.

Some models explicitly calibrate certain parameters with values of either global NPP, or NPP per biome (Cramer et al. 1999). For instance, CASA calibrates a globally uniform value of optimum LUE in the absence of any environmental stresses, using NPP data for about 20 sites. Historically, only a limited number of compilations of NPP per biome, for instance the one by Whittaker & Likens (1975), have been used for model calibration and evaluation. Given the paucity of suitable experimental data, the foundation for moving away from these reference NPP values is very shaky (but see Cramer et al. 1999; for a discussion of more recent data available for model calibration or testing).

Figure 3(a) also clearly segregates the models with NDVI-derived APAR from those with modelled APAR (SIB2 is not in this analysis because incident PAR, being simulated within a coupled General Circulation Model, differs from the data used by the other models). The average NDVI-derived APAR (for CASA, GLO-PEM, SDBM, and TURC) is $94 \times 10^{18}$ J year$^{-1}$, and the average modelled APAR (for BIOME3, CARAIB, FBM, HYBRID, KGBM, PLAI and SILVAN) is $120 \times 10^{18}$ J year$^{-1}$ (Table 1). The difference between NDVI-derived APAR and modelled APAR is significant: standard deviations are 6.9 and 13.5, respectively, and the t-test significance for different means is 0.997.

Zonal profiles

NPP and APAR share the same double-peak pattern (Fig 4a,b), while latitudinal variations of LUE are smaller (Fig 4c), the same order of magnitude as intermodel variations. Thus, the analysis of zonally averaged factors provides another indication that variations of NPP within models are determined by APAR on a first order, while variations of NPP among models are determined by LUE$^3$. GLO-PEM is an exception, as it presents obvious maxima for mid- to high-latitudes, and minima for the seasonal tropics, much like the latitudinal variations of NPP and APAR. Only for GLO-PEM is LUE a significant factor in explaining spatial variations of NPP.

3 The covariation of NPP and APAR, zonally averaged, reflects in part the latitudinal land distribution. Similar results would however, be obtained if NPP and APAR were compared per unit surface area (not shown).
The ‘resource balance perspective’ (Field et al. 1995) can explain why models with a very different structure predict similar patterns of APAR. In this perspective, all environmental resources should be equally limiting to growth, so that plants never invest in more light harvesting than they can utilize for growth. As a consequence, APAR should be related to whatever resource limits growth. In addition, soil nutrients and ecosystem structure adjust in response to climate over long time-scales. Thus, whatever the general approach used in the NPP model, i.e. whether NPP is determined primarily by climate, nutrient availability or vegetation type, similar spatial patterns of APAR are expected. In fact, two global models out of 17 in the intercomparison do not use solar radiation as a driver of plant productivity (Cramer et al. 1999). The main conceptual approach can be statistical relationships between productivity and climate variables, temperature and precipitation for instance, or relationships between carbon assimilation and nutrient availability. Even the outputs of these models do not generally depart significantly from the models analysed here.

The zonal profiles allow us to qualitatively analyse the effects of gradients in some environmental variables (such as water and temperature) on NPP and its component factors. The primary effect of limitations in available resources is to reduce APAR (Fig. 4a,b), while effects on LUE are secondary. Some features are more or less constant in the zonal profiles of LUE (Fig. 4c). In the dry tropics (around 15°N), most models show a dip in LUE, reflecting water shortage. In the equatorial zone (0–10°N), all models, except TURC, show a peak of LUE, reflecting the abundance of environmental resources available for plant productivity (water, light, nitrogen). This can be explained by the fact that all models, except TURC, include stress factors resulting in a reduction of LUE when water, and sometimes also nitrogen, are limited. Important discrepancies among models are visible in Northern temperate and boreal zones (30–60°N). Mean values of LUE are the most different in these latitudes, mostly due to the extremely high LUE for GLO-PEM. In addition, the temperature gradient which characterizes this zone corresponds to either a strong increase (GLO-PEM), a slight increase (HYBRID, TURC, SDBM, PLAI), no significant trend (CARAIB, CASA, FBM, KGBM, SILVAN), or a decrease of LUE (BIOME3). Thus, models generally agree on the effects of water stress on light use efficiency, but do not agree on the effects of temperature.

In addition to differences in model assumptions regarding the effects of stresses, zonal patterns of LUE differ.
may be affected by the calibration of certain model parameters within biomes. For instance, FBM and PLAI calibrate seven coefficients in the processes of GPP, autotrophic and heterotrophic respiration, and litter fall so that mean GPP, NPP and biomass per biome fit mean values for the Matthews (1983) vegetation types reported by Fung et al. (1987). Bondeau et al. (1999) discuss the consequences of calibrating models with NPP per biome. The high LAI of KGBM due to low water constraints leads to high NPP, as the model does not apply any calibration. PLAI and FBM, with a high LAI and therefore a high APAR, calibrate the models with an assumed representative NPP value for the tundra. Thus, low LUE compensates high LAI. We were able to infer a similar effect of compensation between APAR and LUE at the global level, only by displaying the results of many models on the same graph (Fig. 3).

**Discussion**

**Reducing the uncertainty in APAR**

We have seen that spatial patterns of APAR are very similar among models. The main difference is in the overall value of APAR: NDVI-derived APAR is significantly lower than modelled APAR. Different reasons may explain the consistent global 28% discrepancy.

**Underestimation of NDVI-derived FPAR.** The NDVI product has been processed, with some correction of atmospheric effects, calibration, filtering, compositing, and reconstruction where cloud contamination is known to be particularly important ( Sellers et al. 1994). The effect of most of these contaminations is to decrease the satellite signal compared to what could be measured at the surface. Some additional cloud, atmospheric or instrumental contamination may remain after processing (Quadrami et al. 1997). However, the various algorithms used to calibrate the FPAR/NDVI relationship assume that maximum FPAR (in the range 0.9–0.98 depending on the model) corresponds to maximum NDVI, which should correct some of the remaining underestimation of the satellite signal.

**Overestimation of modelled FPAR.** Some models might overestimate LAI because they do not include the whole range of possible constraints on LAI: there is no upper limit, for instance, on the LAI of KGBM provided there is enough water. In addition, some models calibrate some of their relationships so that maximum LAI agrees with literature data, but these data generally come from more productive stands, which could be biased towards high values, and not representative of a 0.5° longitude/latitude grid cell area (see Bondeau et al. 1999).

**Potential vs. actual land cover.** Satellite-derived FPAR corresponds to actual land cover including natural, agricultural and urban areas, while models that compute LAI usually consider potential natural vegetation. Potential vegetation usually has higher FPAR than agricultural and urban areas. Even though crops generally develop a very dense canopy and the resulting APAR could be of the same order as natural vegetation, the active period is shorter for crops compared to grassland or deciduous forest. CARAIB, however, which computes LAI but does incorporate land use, does not support this hypothesis. In regions with little or no land use, it simulates APAR generally closer to satellite-derived APAR than other models simulating LAI, but in regions which are strongly affected by land use, its simulated APAR remains higher than the satellite-derived APAR (results not shown).

Presently, it is not possible to determine the primary cause of the discrepancy. An answer to this question will probably come from improved remote sensing techniques. In the last decade, NDVI derived from NOAA-AVHRR was the only source available to monitor the activity of vegetation from space. New sensors (SEAWiFS, POLDER, VEGETATION, MODIS, etc.), having better resolution, spectral and directional properties, will provide more accurate estimations of land cover and vegetation properties, including FPAR.

**Reducing the uncertainty in LUE**

We have seen that differences in NPP among models are determined by differences in LUE. Light use efficiencies are supposedly not very variable (e.g. Monteith 1972, 1977), so they can be considered a ‘characteristic’ of a vegetation type or a climatic zone, although some scattering and overlapping are reported. In addition, LUE is not a variable used explicitly in CPMs. Thus, values of LUE derived from the literature can constitute an independent check of model behaviour.

Many individual data sets report LUE values for various vegetation types. In addition, several published compilations of values of LUE are available, e.g. Gosse et al. (1986) and Prince (1991) report values for different classes of crops, and Ruimy et al. (1994) report values for natural biomes. Ruimy et al. (1994) report LUE values of natural vegetation types for individual data sets ranging between 0.1 and 0.6 g C MJ⁻¹, and means per biome ranging between 0.2 and 0.5 g C MJ⁻¹. If we assume that the literature values represent ‘reality’, then we can conclude that most models result in ‘realistic’ ranges of LUE, both for individual grid cells (Fig. 2) and for zonal means (Fig. 4). GLO-PEM is an exception, with a much wider range of LUE, from 0.2 to 1.2 g C MJ⁻¹ in zonal means, and an even wider range for individual grid cell values.
The comparison with literature data is limited here to
the overall range of variation, not exact grid cell by grid
cell values or even means per biomes. Indeed, many other
factors, apart from model errors could generate discrep-
cancies between simulated and measured light use
efficiencies:
1 difference in the definition of biomes;
2 difference in the definition of light-use efficiencies (for
instance, literature-derived LUE generally correspond to
above-ground LUE, while model values correspond to
total LUE); and
3 sampling biases in the literature data (because of the
scarcity of data, the values corresponding to mean per
biomes are generally not representative).

More information will come from the development of
techniques for measuring fluxes of CO₂ over whole
Canopies. From these measurements, it is generally
possible to extract light use efficiencies for GPP that are
representative of entire ecosystems, and follow their
seasonal variations (Ruimy et al. 1995).

Conclusion
In this study, 12 global NPP models were analysed. NPP
was decomposed a posteriori into the fraction of PAR
absorbed by the canopy (APAR) and the ratio of NPP to
APAR, or light use efficiency (LUE), to determine which
factor is more important for NPP at different spatial
scales: global, zonal, and at the grid cell level. The spatial
pattern of NPP is determined at the first order by
variations in APAR, and differences in LUE within
models are second-order effects. Thus, all categories of
models can be approximated by a ‘production efficiency
model’, where NPP is the product of APAR and a
constant, model-specific light-use efficiency. Differences
in LUE explain differences in NPP among models. This
situation is complicated by the calibration of certain
model parameters. Explicit or unconscious calibration
seems to occur, with the result that global values of NPP
are within the range of commonly admitted values. If
parameters are calibrated within biomes, the spatial
patterns of NPP could be affected.

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