

Comparing global models of terrestrial net primary productivity (NPP): overview and key results

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Abstract

Seventeen global models of terrestrial biogeochemistry were compared with respect to annual and seasonal fluxes of net primary productivity (NPP) for the land biosphere. The comparison, sponsored by IGBP-GAIM/DIS/GCTE, used standardized input variables wherever possible and was carried out through two international workshops and over the Internet. The models differed widely in complexity and original purpose, but could be grouped in three major categories: satellite-based models that use data from the NOAA/AVHRR sensor as their major input stream (CASA, GLO-PEM, SDBM, SIB2 and TURC), models that simulate carbon fluxes using a prescribed vegetation structure (BIOME-BGC, CARAIB 2.1, CENTURY 4.0, FBM 2.2, HRBM 3.0, KGBM, PLAII 0.2, SILVAN 2.2 and TEM 4.0), and models that simulate both vegetation structure and carbon fluxes (BIOME3, DOLY and HYBRID 3.0). The simulations resulted in a range of total NPP values (44.4–66.3 Pg C year⁻¹), after removal of two outliers (which produced extreme results as artefacts due to the comparison). The broad global pattern of NPP and the relationship of annual NPP to the major climatic variables coincided in most areas. Differences could not be attributed to the fundamental modelling strategies, with the exception that nutrient constraints generally produced lower NPP. Regional and global NPP were sensitive to the simulation method for the water balance. Seasonal variation among models was high, both globally and locally, providing several indications for specific deficiencies in some models.

Keywords: NPP, seasonal, global, model, CO₂

Introduction

Reducing uncertainties in global carbon cycle models

The significant influence of the terrestrial biosphere on the global carbon balance and hence on the problem of timing

and magnitude of possible climate change has been recognized during the past two decades (Bolin *et al.* 1979; Moore *et al.* 1981; Bolin *et al.* 1986; Schimel 1995; Melillo *et al.* 1996). Much of the remaining uncertainty centres on the role of terrestrial ecosystems, in which at least two factors govern the level of carbon storage. First and most obvious is the direct anthropogenic alteration of

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the Earth's vegetation, such as through the conversion of forest to agriculture and the resulting net release of CO₂ to the atmosphere. Second, and more subtle, are the possible changes in net ecosystem production (or the rate of carbon storage) resulting from changes in atmospheric CO₂, other global biogeochemical cycles, and/or the physical-climate system. Gross primary productivity (GPP), net primary productivity (NPP), and heterotrophic respiration (R_H) and their corresponding geographical and seasonal variation are key components in the terrestrial carbon cycle. As highlighted during the international negotiation process for the United Nations Framework Convention on Climate Change, a better grasp upon the controls and distribution of GPP, NPP, and R_H is pivotal for sustainable human use of the biosphere.

At the regional or global scale, none of these fluxes can be observed directly. To improve our understanding of them and to assess the future role of ecosystems in the global context, available local observations need to be scaled to the globe, using physiological and physical principles for the development of global terrestrial ecosystem models. The last few years have seen the emergence of a strategy to improve estimates of terrestrial net and gross primary productivity through measurement and modelling, mainly through the activities of the International Geosphere Biosphere Programme (IGBP), its task forces Global Analysis, Interpretation and Modelling (GAIM) and Data and Information System (DIS), as well as its core project Global Change and Terrestrial Ecosystems (GCTE).

A broad range of models exist now, and they are being used to investigate the magnitude and geographical distribution of primary productivity at the global scale. These models range in complexity from regressions between climatic variables and one or more estimates of biospheric trace gas fluxes to quasi-mechanistic models that simulate the biophysical and ecophysiological processes. Each approach is based on simplifying assumptions about how ecosystems are structured and how vegetation may respond to changes in the environment. Different models use different simplifying assumptions, and they often use different environmental variables, leading to different estimates of global net primary production.

Scaling of carbon and water flux estimates is necessary on three levels:

- 1 from the leaf (where most fluxes can be measured directly using cuvette techniques) to the canopy (Baldocchi & Harley 1995);
- 2 from the 'local' ecosystem (where fluxes from the entire soil-plant system of a small homogeneous area can be measured using micrometeorological techniques) to regions (Running & Hunt 1993; Ruimy *et al.* 1996b); and
- 3 from regions to the globe.

There now is a relatively broad body of experience on the first and second level of scaling (e.g. Jarvis &

Table A. Common abbreviations, symbols and acronyms (NPP model names, cf. Table 1):

| | |
|--------------------------|----------------------------------------------------------------------------------------|
| AET | actual evapotranspiration |
| APAR | absorbed photosynthetically active radiation |
| AVHRR | Advanced Very High Resolution Radiometer |
| AWC | available water capacity |
| DGVM | Dynamic Global Vegetation Model |
| DIS | Data and Information System (IGBP Task Force) |
| ET | evapotranspiration |
| FASIR | Fourier wave Adjustment of NDVI time-series (satellite data product) |
| FC | field capacity |
| Fert | soil fertility factor |
| FPAR | fraction of photosynthetically active radiation absorbed by the canopy |
| G | soil sensible heat flux |
| GAIM | Global Analysis, Interpretation and Modelling (IGBP Task Force) |
| GCM | General Circulation Model |
| GCTE | Global Change and Terrestrial Ecosystems (IGBP Core Project) |
| GPP | gross primary productivity (flux) |
| GPPDI | Global Primary Production Data Initiative |
| GVI | Global Vegetation Index |
| <i>h</i> | relative humidity |
| IGBP | International Geosphere-Biosphere Programme |
| Int | interception |
| ISLSCP | International Satellite Land Surface Climatology Project |
| LAI | leaf area index |
| Leaf-N | nitrogen content of leaves |
| LUE | light use efficiency |
| λ | latitude |
| NDVI | Normalized Difference Vegetation Index |
| NEP | net ecosystem production (annual integral) |
| NPP | net primary productivity (flux – net primary production refers to the annual integral) |
| PAR | photosynthetically active radiation at the top of the canopy |
| PEM | Production efficiency model |
| PET | potential evapotranspiration |
| <i>P</i> | precipitation |
| R _A | autotrophic respiration |
| RD | rooting depth |
| R _H | heterotrophic respiration |
| R _s | solar radiation |
| S | soil inorganic sulphur |
| Soil C & N | both carbon and nitrogen in soil organic matter |
| SW | soil water |
| <i>T</i> | (air) temperature |
| <i>T</i> _{surf} | surface temperature |
| Veg C | vegetation carbon (i.e. carbon in leaves, sapwood, heartwood, roots, etc.) |
| Veg N | nitrogen content in leaves and roots |
| VPD | vapour pressure deficit |
| WBC | water balance coefficient |
| WP | wilting point |

McNaughton 1985; Raupach 1995). The present suite of models represent the third level, since they all incorporate point-based soil-plant models for every cell in a global grid, being driven by global interpolated data bases of environmental conditions and/or satellite observations.

Validating global carbon flux estimates

Since the global flux cannot be measured *per se*, a connection of global model results to measurements is necessary for validation. Direct carbon flux measurements are made at the leaf or canopy level, and regional estimates may be derived as estimates from other sources, such as forest or agricultural yield statistics. Implicit in the application of NPP models across a global grid is the simplifying assumption that process descriptions defined and parameterized from a set of field or laboratory studies are directly applicable to the full range of conditions that occur across the globe. To validate such process models with respect to their broad applicability is not possible in a direct sense. As a minimum, however, models which have been calibrated only for some locations can be tested against data from other locations—if good agreement is achieved then this adds plausibility to the model. Two factors are particularly limiting the diagnostic value of this test:

- 1 the validity of the scaling approach from the canopy to the (heterogeneous) region can be assessed for short-term, aircraft-based measurements only; and
- 2 the test cannot cover the full range of conditions occurring worldwide.

Nevertheless, the existing potential for comparison of model results against measurements has not yet been fully exploited. Another IGBP-sponsored activity (the Global Primary Production Data Initiative, GPPDI) is therefore underway with the aim to provide a globally consolidated data base of NPP observations (Scurlock *et al.*, in press). To be of use for the validation of global models, it is not sufficient to simply assemble all available observations into one data base. Even at their respective scale level, most NPP data are derived from measurements of other quantities, such as biomass over time, and frequently do not fully capture below-ground processes. Therefore, the validity of each individual estimate with respect to the local scaling from the measurement to the region, and from the timing of the measurement to the mean climatic situation needs to be checked for every data point. Once this process (which takes considerable time and effort due to the requirement of careful data screening and quality assessment) is completed, a new round of comparison between NPP model outputs and ground observations could be carried out.

An alternative approach to validation of the global flux is to aggregate estimates of net ecosystem production (NEP), i.e. the change in total carbon storage by ecosystems over time, using an atmospheric transport model and to compare the resulting CO₂ concentrations with those measured by the international station network. This approach is not without limitations in itself, since it relies on the assumptions and underlying data of the transport model as much as on the biogeochemical models, but it provides a valuable alternative to measure-

ments as model test (Heimann *et al.* 1998; Nemry *et al.* 1999).

Testing models by comparison

As a surrogate for the direct validation, model comparisons have frequently been used to check the applicability of various kinds of models (e.g. Ågren *et al.* 1991; Cess *et al.* 1991; Randall *et al.* 1994; VEMAP Members *et al.* 1995; 1996b; Ryan *et al.* 1996a). The potential of such intercomparisons comes mainly from the fact that they can highlight model weaknesses and inconsistencies, but it must be emphasized that they cannot provide direct validation (Rastetter 1996).

The model intercomparison described by the papers in this issue was the first for total biospheric flux estimates at the global scale. It was carried out during two workshops at the Potsdam Institute of Climate Impact Research (PIK) in June 1994 and in July 1995, which were followed by joint activities of modelling and writing teams, using a dedicated database of model input data and results, hosted at PIK. This paper is the introduction and summary of a series of papers that present results from the second intercomparison workshop. It gives a brief overview over the main categories of models that were part of the comparison, as well as discussing their underlying approaches. We then document the standardization of data sets and other basic features common to all models. We present some global results and, finally, summarize some of the key findings from the teams who contributed papers to this series.

Modelling approaches

Basic model assumptions

The carbon exchange between the terrestrial biosphere and the atmosphere is primarily controlled by solar radiation and by the local environment, i.e. by the conditions under which plants can photosynthesize and then allocate photosynthate to various components and by the environmental conditions influencing the decomposition of dead plant material. Precipitation and temperature are the two major climatic factors that govern the absorption of photosynthetically active radiation (PAR) and the associated conversion of CO₂ into dry matter, i.e. the net primary productivity (NPP) of the biosphere.

The first NPP model (MIAMI, Lieth 1975) used an empirical regression to relate annual NPP to the annual average (bio)temperature and precipitation without any accounting for solar radiation nor ambient CO₂ concentration. Because of its simplicity and its empirical basis, this model is still used as a baseline for evaluation while more sophisticated mechanistic models are developed. A 'modernized' version of it is the High Resolution Biosphere Model (HRBM, Esser *et al.* 1994), which

Table 1 List of participating models, modelling teams and References, listed in alphabetic order

| Full name (if any) | | Host Institution | Key References |
|--------------------|--------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------|
| BIOME3 | | Department of Ecology, Lund University, Sweden | Haxeltine & Prentice 1996; Haxeltine <i>et al.</i> 1996 |
| BIOME-BGC | Biome BioGeochemical Cycles model | School of Forestry, University of Montana, Missoula, MT, USA | Running & Hunt 1993 |
| CARAIB 2.1 | CARBOn Assimilation In the Biosphere model | Laboratory for Planetary and Atmospheric Physics, Liège University, Liège, Belgium | Warnant <i>et al.</i> 1994; Nemry <i>et al.</i> 1996 |
| CASA | Carnegie Ames Stanford Approach model | Carnegie Institute of Washington, Stanford University, Stanford, CA, USA | Potter <i>et al.</i> 1993; Field <i>et al.</i> 1995 |
| CENTURY 4.0 | | University of Colorado, Fort Collins, Colorado, USA | Parton <i>et al.</i> 1993 |
| DOLY | | Department of Plant and Animal Sciences, Sheffield University, Sheffield, UK & Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA | Woodward <i>et al.</i> 1995 |
| FBM 2.2 | Frankfurt Biosphere Model | Department of Theoretical and Physical Chemistry, Johann-Wolfgang-Goethe University, Frankfurt/Main, Germany | Kindermann <i>et al.</i> 1993; Lüdeke <i>et al.</i> 1994; Kohlmaier <i>et al.</i> 1997 |
| GLO PEM | GLOBAL Production Efficiency Model | Department of Geography, University of Maryland, MD, USA | Prince 1991; Prince & Goward 1995 |
| HRBM 3.0 | High Resolution Biosphere Model | Department of Plant Ecology, Justus-Liebig-University, Gießen, Germany | Esser <i>et al.</i> 1994 |
| HYBRID 3.0 | | Institute of Terrestrial Ecology, Edinburgh, UK | Friend 1995; Friend <i>et al.</i> 1997 |
| KGBM | Kergoat Global Biosphere Model | Laboratory of Terrestrial Ecology, Toulouse, France | Kergoat 1998 |
| PLAI 0.2 | Potsdam Land Atmosphere Interaction Model | Potsdam Institute for Climate Impact Research, Potsdam, Germany | Plöchl & Cramer 1995a+b |
| SDBM | Simple Diagnostic Biosphere Model | Max-Planck Institute for Meteorology, Hamburg, Germany | Knorr & Heimann 1995 |
| SIB2 | Simple Interactive Biosphere Model | NASA/Goddard Space Flight Center, Greenbelt, MD, USA | Sellers <i>et al.</i> 1996a+b; Randall <i>et al.</i> 1996 |
| SILVAN 2.2 | Simulating Land Vegetation And NPP model | Max-Planck-Institute for Meteorology, Hamburg, Germany | Kaduk & Heimann 1996 |
| TEM 4.0 | Terrestrial Ecosystem Model | University of Alaska, Fairbanks, AK, USA The Ecosystems Center, MBL, Woods Hole, MA, USA Complex Systems Research Center, Durham, NH, USA | McGuire <i>et al.</i> 1995; McGuire <i>et al.</i> 1997 |
| TURC | Terrestrial Uptake and Release of Carbon | Laboratoire d'Ecophysiologie Végétale, Orsay, France | Ruimy <i>et al.</i> 1996 |

participated in the present comparison. To account for the ecophysiological and biophysical processes that determine the spatio-temporal features of NPP with a goal of providing prognostic capabilities, more complex models have been developed. Mechanistic relationships are used to describe the fluxes of CO₂ (all models), water (most models), and nutrients (few models) between the different compartments of vegetation, soil and atmosphere. The major processes are: photosynthesis, growth and maintenance respiration, evapotranspiration, uptake and release of nitrogen, allocation of photosynthate to the various parts of the plant, litter production and decomposition, and phenological development.

The 17 models¹ analysed in the intercomparison are listed in Table 1, with their key references. Although all

models estimate NPP, most of them are primarily developed for other purposes, e.g. to examine past or future changes in total carbon fluxes and/or storage, or to test particular hypotheses about the underlying causes of these changes. Three major groups of models are identified (Table 2), based on whether the models use a prescribed seasonal behaviour of light interception by the canopy and/or a prescribed vegetation distribution. The three categories use different generic approaches to assess the effect of climate on NPP.

1 The first group uses satellite data to determine the temporal behaviour of the photosynthetically active tissue. These models can be used to examine the effect of climate variability on NPP, but the time of interest is limited to that of the satellite archive (Maisongrande *et al.* 1995; Malmström *et al.* 1995; Kindermann *et al.* 1996). From the satellite observations, they provide some certainty for the seasonal dynamics (phenology) of biospheric production.

2 The second group simulates the biogeochemical fluxes on the basis of soil and climate characteristics, using either vegetation maps or biogeography models to prescribe vegetation structure. With one exception, these

¹ The Simple Diagnostic Biosphere Model (SDBM, Knorr & Heimann 1995) provided outputs for the first Potsdam NPP Model intercomparison (1994) only. Since some of the input data could not be standardized, the SDBM outputs have generally not been considered in the analysis of the intercomparison. Some SDBM results, however, are discussed in accompanying papers (Bondeau *et al.* 1999; Nemry *et al.* 1999; Ruimy *et al.* 1999).

models simulate phenology either explicitly or implicitly so that the seasonal activity of the canopy can change in response to climate change. Such models can only describe functional changes *within* particular vegetation types and thereby ignore the possible effects of (slow) vegetation redistribution.

3 The third group simulates changes in both ecosystem structure (vegetation distribution and phenology) and function (biogeochemistry). Generally, equilibrium between climate and vegetation is assumed, but the models can be turned into dynamical global vegetation models (DGVMs). To date, they have been applied to potential vegetation only. This is in contrast to some of the models in the other categories which account for land use either explicitly (CARAIB) or implicitly through the use of satellite observations.

The models use different input data sets to represent global climate, vegetation and soils (when needed). For the comparison, most input data sets have been standardized (see 'Methods: Common data sets' below), but this was not possible in all cases. For example, a model that requires a known vegetation distribution must use a global vegetation map (or an estimate from a biogeography model) which is in agreement with its modelling strategy, while others may use either different vegetation classes or no map at all. In addition, the input data sets used by model developers vary in spatial and temporal resolution (Table 3, columns 2–3).

The major model features are listed in Table 3. Two basic approaches are used to calculate NPP (Table 3, column 4). Some models (e.g. CASA, CENTURY and HRBM) relate NPP directly to vegetation characteristics and environmental variables or indicators such as temperature, precipitation, soil nitrogen or fertility factors. Others estimate NPP as the difference between two processes which are modelled independently: gross primary productivity (GPP: the uptake of carbon from the atmosphere by plants), and autotrophic respiration (R_A : the release of carbon to the atmosphere by plant respiration). In the latter case, the environmental and structural variables influence GPP and R_A instead of NPP.

The relative influence of different driving variables on NPP varies among models (Table 3, column 5). Most models simulate the influence of solar radiation (R_s , generally represented through PAR) on NPP. CENTURY and HRBM, however, do not explicitly consider solar radiation—its influence is implicitly included in the effects of temperature or self-shading on NPP. With the exception of TURC, all models simulate the influence of water availability on NPP using soil water status and/or vapor pressure deficit (Churkina *et al.* 1999). In BIOME-BGC, DOLY, HYBRID, and TEM, GPP and/or R_A depend on nutrient availability. In CENTURY and HRBM nutrients affect NPP directly.

Because the storage of carbon in vegetation is represented differently among the models (Table 3,

Table 2 Categories of participating NPP models, defined on the basis of required input and typical output variables

| | Selected inputs ^a | | | Selected outputs | | |
|--------------------------------------------------------------------|--------------------------------------|----------------|-----------------------------------|-----------------------|------------------------------------|-------------------------|
| | Vegetation distribution ^b | Satellite FPAR | Other satellite data ^c | Biogeochemical fluxes | Leaf Area Index (LAI) ^d | Vegetation Distribution |
| Satellite based models | | | | | | |
| CASA | X | X | | X | | |
| GLO-PEM | | X | X | X | | |
| SDBM | | X | | X | | |
| TURC | X | X | | X | | |
| SIB2 | X | X | X | X | | |
| Models for seasonal biogeochemical fluxes | | | | | | |
| HRBM | | | | X | | |
| CENTURY | X | | | X | | |
| TEM | X | | | X | | |
| CARAIB | X | | | X | X | |
| FBM | X | | | X | X | |
| PLAI | X | | | X | X | |
| SILVAN | X | | | X | X | |
| BIOME-BGC | X | | | X | X | |
| KGBM | X | | X | X | X | |
| Models for seasonal biogeochemical fluxes and vegetation structure | | | | | | |
| BIOME3 | | | | X | X | X |
| DOLY | | | | X | X | X |
| HYBRID | | | | X | X | X |

^a Since climate is a common input to all models, it is not listed in a separate column here. ^b TURC uses biomass data based on Olson *et al.* (1985). Other models use vegetation types to stratify parameters. ^c GLO-PEM uses satellite data to estimate photosynthetically active radiation (PAR), surface temperatures, soil moisture, vapour pressure deficit and above-ground biomass. SIB2 uses satellite data to estimate LAI, roughness length and albedo. KGBM uses satellite-derived NDVI data to determine the timing and length of the growing season. ^d BIOME3 uses foliar projected cover (FPC) instead of LAI.

column 6), several approaches are used to estimate GPP, R_A and NPP. For example, some models use only one single pool of carbon (e.g. TEM) with a single equation describing either GPP, R_A , or NPP, whereas other models (e.g. CENTURY) allocate carbon to many pools (e.g. leaves, sapwood, heartwood, fine roots) and estimate respiration and the accumulation of carbon, either by GPP or allocation.

The following sections provide some more detail on the different models within each category.

Remote sensing based models

The appearance of global data sets from satellites like the NOAA/AVHRR since the late 1970s has provided new opportunities for the global monitoring of the temporal variation of terrestrial ecosystems. The linkage between Vegetation Indices (VIs), which are various combinations of the satellite measurements in the red and near infrared bands, and the fraction of canopy-absorbed photosynthetically active radiation (FPAR, cf. Kumar & Monteith 1981; Sellers 1985; Sellers 1987; Goward & Huemmrich 1992) provides

Table 3 Comparison of the broad features of the participating NPP models

| | NPP | | | No. of VEGC pools | Strategy | Calibrated |
|-------------|------------------------|------------------|-----------------------------------------------------------------------------------------------|-------------------------|--------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------|
| | temporal resolution | calculated as | influenced by | | | |
| CASA | 1 month | NPP | $NPP = f(R_s, FPAR, T, AET/PET)$ | 0 | PEM, LUE derived empirically, applied to NPP | NPP |
| GLO-PEM | 10 days | GPP- R_A | $GPP = f(R_s, FPAR, T, SW, VPD)$ $R_A = f(Veg\ C, GPP)$ | 2 | PEM, LUE derived from a mechanistic model, applied to GPP | N/A |
| SDBM | 1 month | NPP | $NPP = f(R_s, FPAR, CO_2)$ | 0 | PEM, LUE derived empirically, applied to NPP | CO ₂ (using an atmospheric transport model) |
| TURC | 1 month | GPP- R_A | $GPP = f(R_s, FPAR)$ $R_A = f(Veg\ C, T)$ | 3 | PEM, LUE derived empirically (global value), applied to GPP, environmental constraints applied to R_A | N/A |
| SIB2 | 12 min | GPP- R_A | $GPP = f(R_s, FPAR, LAI, T, SW, VPD, CO_2)$ $R_A = f(GPP, T, SW)$ | 2 | SVAT model, coupled to GCM | N/A |
| HRBM | 1 month | NPP | $NPP = f(T, P, AET/PET, CO_2, Fert)$ | 0 | regression of annual NPP on climate, seasonality driven by AET | NPP |
| CENTURY | 1 month | NPP | $NPP = f(Veg\ C, T, SW, P, PET, N, P, S)$ | 8 | mechanistic soil C and N model with above – ground vegetation processes, calibrated against observations | NPP |
| TEM | 1 month | GPP- R_A | $GPP = f(R_s, KLeaf, T, AET/PET, CO_2, N)$ $R_A = f(Veg\ C, GPP, T)$ | 1 | mechanistic process model, using climate and soils data with a water balance algorithm to estimate NPP | NPP |
| CARAIB | 1 day | GPP- R_A | $GPP = f(R_s, LAI, T, SW, VPD, CO_2, O_2)$ $R_A = f(Veg\ C, LAI, T)$ | 2 | leaf level photosynthesis model, C and H ₂ O balance integrated over the canopy, phenology internal | NPP |
| FBM | 1 day | GPP- R_A | $GPP = f(R_s, LAI, T, SW, CO_2)$ $R_A = f(Veg\ C, T)$ | 2 | leaf level photosynthesis model, C and H ₂ O balance integrated over the canopy, phenology internal | NPP |
| PLAI | 1 day | GPP- R_A | $GPP = f(R_s, LAI, T, SW, CO_2)$ $R_A = f(Veg\ C, T)$ | 2 | leaf level photosynthesis model, C and H ₂ O balance integrated over the canopy, phenology internal | NPP |
| SILVAN | 6 days | GPP- R_A | $GPP = f(R_s, LAI, T, AET/PET, CO_2)$ $R_A = f(Veg\ C, T)$ | 3 | leaf level photosynthesis model, C and H ₂ O balance integrated over the canopy, phenology internal | NPP |
| BIOME – BGC | 1 day | GPP- R_A | $GPP = f(R_s, LAI, T, SW, VPD, CO_2, Leaf\ N)$ $R_A = f(Veg\ C, T)$ | 4 | estimates LAI from water balance, no phenology | N/A |
| KGBM | 1 day | GPP- R_A | $GPP = f(R_s, LAI, T, SW, VPD)$ $R_A = f(GPP)$ | 1 | estimates LAI from water balance, phenology (= inactive period) from satellite | N/A |
| BIOME3 | 1 month | GPP- R_A | $GPP = f(R_s, LAI, T, AET/PET, CO_2)$ $R_A = f(LAI, GPP)$ | 0 | simulates vegetation structure and physiological processes, coupled C and H ₂ O balance, phenology internal | N/A |
| DOLY | 1 year | GPP- R_A | $GPP = f(R_s, LAI, T, SW, VPD, CO_2, Soil\ C\ \&\ N)$ $R_A = f(Veg\ C, T, Soil\ C\ \&\ N)$ | 2 | simulates vegetation structure and physiological processes, coupled C and H ₂ O balance, R_A and NPP annual | N/A |
| HYBRID | 1 day | GPP- R_A | $GPP = f(R_s, FPAR, T, SW, CO_2, N)$ $R_A = f(Veg\ C, T, Veg\ N)$ | 4 | simulates vegetation structure and physiological processes, coupled C and H ₂ O balance, phenology internal | N/A |

the absorbed photosynthetically active radiation (APAR), and thereby connects satellite observations to biological productivity on large scales (Maisongrande *et al.* 1995). The 'Production Efficiency Models' (PEMs) use the concept of light use efficiency² (LUE) for the conversion of APAR to biomass. Since, under ideal conditions, the rate of primary production is linearly related to PAR absorption (Monteith 1977; Landsberg 1986), LUE can be regarded as a conservative quantity, which can be used to scale the integral of $FPAR \times PAR$ (over the growing season) to primary production. This concept is suitable for use with remotely sensed observations which provide both the timing of the active period and the quantitative values of FPAR.

² We acknowledge that the term 'efficiency' for this quantity is technically somewhat imprecise. It is, however, so well-established in the relevant literature that we opted to not use a different terminology. For further discussion of this concept, see Ruimy *et al.* (1999).

Actual production varies depending on the environment and between plants with different photosynthetic pathways and respiration rates (Jarvis & Leverenz 1983; Prince 1991). Therefore, some models combine the PEM structure with more classical process based formulations, including nutrient cycling and photosynthetic controls, to estimate the variability of the LUE. These models have very different levels of mechanism in the description of the effects of the environment on LUE. Some apply the LUE concept to NPP (CASA, SDBM), others to GPP. In most PEMs (CASA, TURC, SDBM), the potential LUE value is empirically derived and then reduced due to environmental constraints.

GLO-PEM is unique among all models by not using any climatic driving variables observed on the ground (except for distinguishing between C₃ and C₄ grasses). All variables about climate and vegetation structure are derived from satellite observations. SIB2, despite being a remote sensing based model, is not a PEM: fluxes are simulated at the leaf level and then

Table 4 Input variables required by the different models (data for calibration are not included)

| Veget. type | | Soil | | Climate | | | | | | | | | | Net rad. | Wind speed |
|-------------|------------|--------------|--------------|--------------|--------|-------|--------------------|---------|-------------|----|----------|--------------|----------------|--------------------|------------|
| map | climate | type/texture | r. depth | WHC | C, N | elev. | [CO ₂] | Atm. | mean T | ΔT | P | humidity | R _s | | |
| CASA | a [D & S] | text [FAO/Z] | f(veg) | | [Po] | | 360 | m [F87] | m [CL] | | m [CL] | | m (λ, c[CL]) | | |
| GLO-PEM | | %text [W] | 1 m | constant | | | 34 Pa | [F87] | 10d (Pathf) | | * | 10d (Pathf) | m (TOMS) | | |
| SDBM | | | | | | | | m [G] | m [CL] | | m [CL] | | m (λ, c[CL]) | | |
| TURC | | | | | | | | m [F87] | m [CL] | | | | m (λ, c[CL]) | | |
| SIB2 | a [Ma, K] | text [FAO/Z] | X | f(t) | | X | 35 Pa | m [F87] | h (GCM) | | h (GCM) | h (GCM) | h (GCM) | | |
| HRBM | p (B) | t [FAO] | | f(t) | | | 340 | | m [CL] | | m [CL] | | m (λ, c[CL]) | | h (GCM) |
| CENTURY | p [Me] | %text [FAO] | f(veg) | f(text) | | | 340 | | m [CL] | | m [CL] | | m (λ, c[CL]) | | |
| TEM | p [Me] | %text [FAO] | | f(text, veg) | | X | 340 | | | | | | | | |
| CARAIB | a [W & HS] | text [FAO/Z] | f(t,veg) | constant | | X | 350 | | d [CL + wg] | | d (wg) | d (FC,PWP) | d (λ, c[CL]) | | |
| FBM | p [Ma] | text [FAO/Z] | f(text, veg) | f(text, veg) | | | 350 | | d [CL] | | d f(veg) | | d (λ, c[CL]) | | |
| PLAI | p (B) | text [FAO/Z] | | f(text) | | | 350 | | d [CL] | | d [CL] | | d (λ, c[CL]) | | |
| SILVAN | p (B) | %text [W] | [W] | constant | | | 340 | | d [CL] | | d [CL] | | d (λ, c[CL]) | | |
| BIOME-BGC | p (B) | text [FAO/Z] | 2 m | f([W & HS]) | | X | 340 | | d [CL] | | d (WGEN) | | d [R] | | |
| KGBM | p [Ma] | text [FAO/Z] | f(veg) | f(text) | | | 340 | w [C86] | d [CL] | | d [CL] | d vp [S & J] | d (λ, c[CL]) | f(R _s) | |
| BIOME3 | | text [FAO/Z] | 1.5 m | f(text) | | | 340 | | d [CL] | | d [CL] | | d (λ, c[CL]) | | |
| DOLY | | constant | | | [Z,Po] | | 350 | | d [CL] | | d [CL] | | d [H] | | |
| HYBRID | | | f(Soil-C) | f(Soil-C) | [Pa] | | 280 | | d (WGEN) | | d (WGEN) | d (WGEN) | d (WGEN) | | |

Vegetation type: a: actual vegetation; p: potential vegetation; [D & S]: derived from Dorman & Sellers (1989); [Ma]: derived from Matthews (1983); [Me]: from Melillo *et al.* (1993); [Ma, K]: derived from Matthews (1983) and Küchler (1983); [W & HS]: derived from Wilson & Henderson-Sellers (1985); (B): BIOME1 model (Prentice *et al.* 1992), BIOME-BGC assigns functional types to the biomes.

Soil type/texture: t: soil type; text: texture categories; %text: percentage of sand, silt and clay; [FAO]: FAO/UNESCO (1974); [FAO/Z]: Zobler (1986); [W]: derived from Webb *et al.* (1992).

Rooting depth: function of soil type (t), vegetation type (veg), soil carbon (Soil-C); [W]: derived from Webb *et al.* (1992).

Soil water holding capacity (WHC): function of soil type (t), soil texture (text), vegetation type (veg), soil carbon (Soil C); [W & HS]: derived from Wilson & Henderson-Sellers (1985); Soil C, N: [Pa]: Parton *et al.* (1993); [Po] Post *et al.* (1982, 1985); [Z]: Zinke *et al.* (1984).

Atmospheric [CO₂]: in ppmv if not otherwise indicated NDVI: m: monthly, w: weekly; [F87]: ISLSCP-FASIR 1987 (Los *et al.* 1994); [G]: 3 years average from Gallo (1992); [C86]: CESBIO 1986 (Berthelot *et al.* 1994).

Climate: m: monthly inputs required; d: daily inputs available or interpolated; h: hourly inputs; [CL]: monthly mean temperature T, temperature range ΔT, precipitation P, and sunshine hour percentage from the standard CLIMATE database (updated version of Leemans & Cramer 1991); [CL + wg]: daily interpolation using the weather generator of the model; WGEN: Friend (1998); [L]: Leemans, personal communication; (GCM): derived from a GCM; (λ, c[CL]): derived from latitude and cloudiness (Otto *et al.* unpublished data); (TOMS): satellite PAR estimates (Dye & Shibasaki 1995); [H] or [R]: microclimate simulator (Running *et al.* 1987; Hungerford *et al.* 1989); vp [S & L] vapour pressure derived from Spangler & Jenne (1990); 10d (Pathfinder): derived from the decadal AVHRR Pathfinder 1987 data set (Agbu & James 1994).

*: GLO-PEM estimates soil moisture directly from the AVHRR data set, without requirement of data on soil and precipitation.

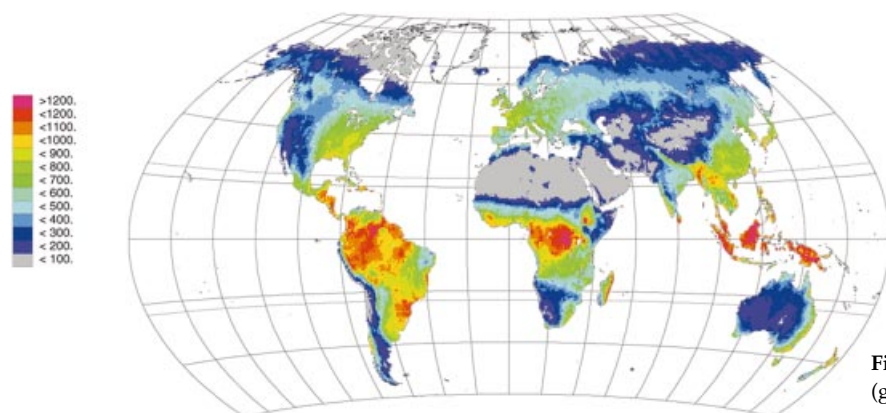


Fig. 1 Annual net primary production (g C m^{-2}) estimated as the average of all model NPP estimates.

integrated over the canopy, therefore the production is not linearly related to canopy APAR through a light use efficiency. It is a soil-vegetation-atmosphere-transfer (SVAT) model and simulates land surface processes in detail and with short time steps (minutes) and coarse spatial resolution (4° latitude \times 5° longitude) coupled to a General Circulation Model. Several parameters are derived from satellite data, including roughness length, albedo, FPAR and LAI.

Models of seasonal biogeochemical fluxes

All models in this category use climate and soils data as input variables. Vegetation distribution (either from one of several available maps or from the climate-based BIOME model, Prentice *et al.* 1992) is required for the parameterization of some processes. The level of process mechanism is very different between these models, ranging from the largely empirical regression model HRBM to several different explicitly mechanistic models including photosynthesis and respiration (cf. Tables 3 and 4). Some models in this category use satellite data as well, but only for the calibration or prescription of some processes.

Models of process and pattern (function and structure)

The three models in this class (BIOME3, DOLY, and HYBRID) all simulate biogeochemical processes (fluxes) and pattern (vegetation type and structure) simultaneously. The determination of the vegetation types follows process optimization rules (maximization of the NPP according to soils and climate, or maximization of the LAI to satisfy the annual moisture and carbon balances). The results are not calibrated—the parameter values for individual process descriptions are chosen from the literature. CO_2 fluxes are simulated at hourly/daily time steps and directly coupled with water fluxes. HYBRID is the only nonequilibrium model of the comparison—it applies a gap-model strategy with explicit growth formulations at the global scale. It therefore is a Dynamic Global Vegetation Model

(DGVM), capable of predicting the response of vegetation to climate change, due to the dynamic coupling of the temporal changes of both structure (like LAI) and function (like the fluxes of carbon, water and nutrients).

Methods for the comparison

Comparison strategy

During and after the Potsdam workshops, model comparisons were carried out by a combination of standardized model runs and subsequent analyses by working groups. The main strategy was to confront all modelling teams with all output data sets from all models, using a visualization tool which allowed comparisons to take place with identical cartographic features (geographical projection, colour scales, etc.). The data were collected from all teams prior to the workshops and reformatted to a standard format for on-line analysis and visualization, during and after the workshop. The global results are shown in the next section. Six working groups addressed special issues across several models. Their results are presented in separate papers in this issue (Bondeau *et al.* 1999; Churkina *et al.* 1999; Kicklighter *et al.* 1999; Nemry *et al.* 1999; Ruimy *et al.* 1999; Schloss *et al.* 1999).

Common data sets

Full standardization of all input data sets, spatial scale assumptions, etc. is not achievable for a broad comparison of this type. We nevertheless aimed for the highest possible level of standardization using a common spatial framework for most data sets.

Being climate-driven, all NPP models require data on temperature and moisture availability. All models (except GLO-PEM, spatial resolution $8\text{ km} \times 8\text{ km}$, and SIB2, $4.0^\circ \times 5.0^\circ$) already used climate data sets gridded at 0.5° longitude/latitude resolution—GLO-PEM was run at that resolution to allow direct comparison at the workshop. Again, apart from GLO-PEM and SIB2, all models use monthly long-term means of climatic variables (those

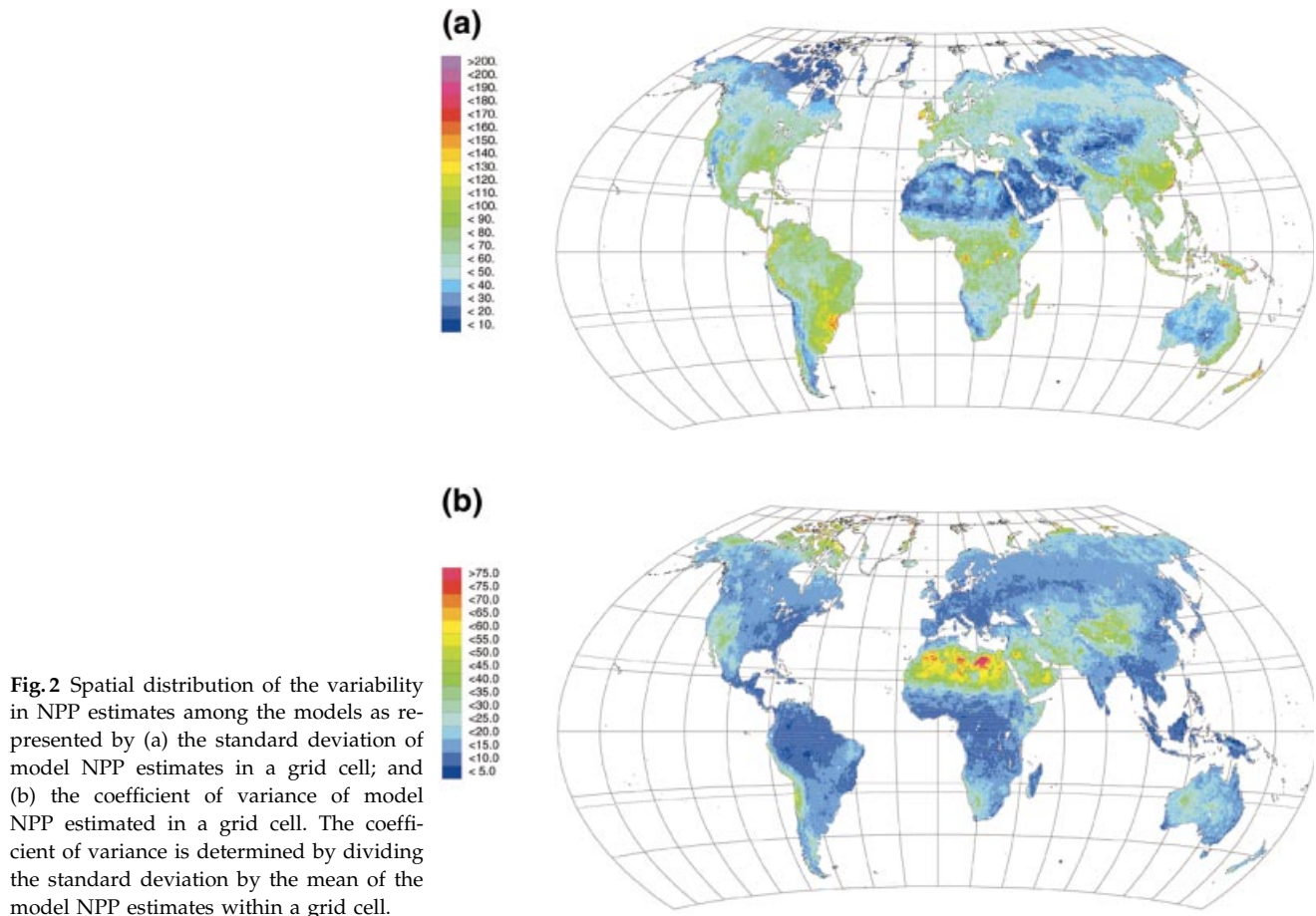


Fig. 2 Spatial distribution of the variability in NPP estimates among the models as represented by (a) the standard deviation of model NPP estimates in a grid cell; and (b) the coefficient of variance of model NPP estimated in a grid cell. The coefficient of variance is determined by dividing the standard deviation by the mean of the model NPP estimates within a grid cell.

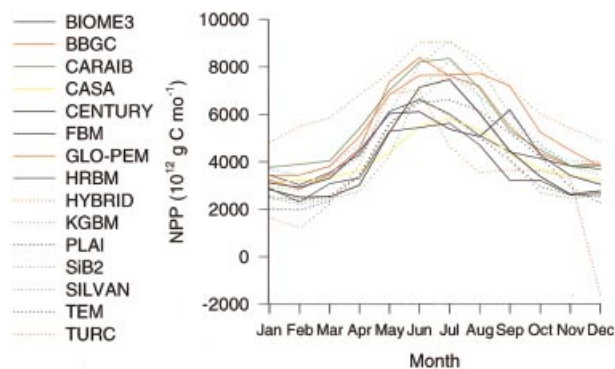


Fig. 3 Comparison of seasonal variations in global net primary productivity among all models except DOLY, which simulated only annual totals.

running at daily time steps usually generate quasi-daily climate data from monthly averages internally). A few models interpolate quasi-hourly climate data for estimating GPP whereas others (e.g. CARAIB, HYBRID) apply weather generators (Friend 1998; Hubert *et al.* 1999) to simulate daily variability. The CLIMATE data base (long-term means 1931–60, version 2.1, Leemans & Cramer 1991; W. Cramer *et al.* unpublished data) was used by all participants for monthly mean air temperatures and

precipitation values. Unless indicated otherwise, temperature concerns air temperature throughout the comparison.

Solar radiation is required by most models, but the formulations for estimating it differ among the models. Some models estimate radiation from latitude and cloudiness using gridded sunshine hour percentages as a proxy for cloudiness from the CLIMATE data base (R.D. Otto *et al.* unpublished data). SIB2 is linked to a General Circulation Model and derives solar radiation from that model. To simplify model comparisons, it was suggested that those models that require satellite data for the quantitative prescription of seasonal changes in FPAR all use the FASIR data set for 1987 of the ISLSCP CD-ROM database (Sellers *et al.* 1994; Meeson *et al.* 1995). This data set consists of monthly NDVI at a spatial resolution of 1° with improved processing compared to the standard GVI product widely used before. However, not all satellite-based models were developed using the FASIR data set—their adaptation to it for the comparison resulted in weaker performance. GLO-PEM, for example, was designed to use satellite data at a higher temporal and spatial resolution (AVHRR Pathfinder) that provide other information (e.g. surface temperature, humidity) that are not available from the FASIR data set. Therefore, the

Table 5 Comparison of annual and monthly global NPP and the factors influencing NPP among 16 models, ranked in decreasing order of global annual NPP estimates

| | Annual NPP (Pg C) | Number of grid cells | Area (10 ⁶ km ²) | Mean length of growing season (months) ^a | Monthly maximum NPP (Pg C) | Monthly minimum NPP (Pg C) | Seasonal range in NPP (Pg C months ⁻¹) | Temporal resolution of NPP | Veg ^b | NDVI | Moisture ^c | Nutrient Constraints ^d |
|-----------|-------------------|----------------------|-----------------------------------------|-----------------------------------------------------|----------------------------|----------------------------|----------------------------------------------------|----------------------------|------------------|-----------------|-----------------------|-----------------------------------|
| TURC | 80.5 | 56785 | 128.7 | 10.5 | 9.1 | 4.8 | 4.3 | monthly | A | FPAR | | |
| GLO-PEM | 66.3 | 56785 | 128.7 | 6.0 | 7.7 | 3.4 | 4.3 | monthly | A | FPAR and others | SW, VPD | |
| CARAIB | 65.2 | 56785 | 128.7 | 6.3 | 8.4 | 3.8 | 4.6 | daily | A(M) | | SW, VPD | |
| KGBM | 62.5 | 56785 | 128.7 | 6.4 | 9.1 | 2.8 | 6.3 | daily | P(D) | PHENO | SW, VPD | |
| BIOME-BGC | 62.2 | 54279 | 124.0 | 6.2 | 8.4 | 2.9 | 5.5 | daily | P(D) | | SW, VPD | Leaf-N |
| SILVAN | 61.1 | 56785 | 128.7 | 6.8 | 7.7 | 3.5 | 4.2 | 6 days | P(D) | | AET/PET | |
| BIOME3 | 54.2 | 56785 | 128.7 | 7.5 | 6.6 | 3.0 | 3.6 | monthly | P(M) | | AET/PET | |
| CENTURY | 53.3 | 50641 | 116.9 | 8.3 | 6.2 | 2.9 | 3.3 | monthly | P(B) | | SW, P | N, P, S |
| FBM | 49.9 | 47807 | 105.6 | 7.4 | 7.5 | 2.5 | 5.0 | daily | P(B) | | SW | |
| PLAI | 49.2 | 56785 | 128.7 | 5.2 | 6.6 | 2.0 | 4.6 | daily | P(B) | | SW | |
| CASA | 48.9 | 56785 | 128.7 | 9.1 | 5.8 | 3.1 | 2.7 | monthly | A(D) | FPAR | AET/PET | |
| SIB2 | 47.9 | 51050 | 115.7 | 7.1 | 8.3 | 2.2 | 6.1 | 12 min | A(D) | FPAR and others | SW, VPD | |
| DOLY | 46.4 | 56785 | 128.7 | N/A ^e | N/A | N/A | N/A | annual | P(D) | | SW, VPD | Soil C & N |
| TEM | 46.2 | 55290 | 125.6 | 6.8 | 6.7 | 2.4 | 4.3 | monthly | P(B) | | AET/PET | N |
| HRBM | 44.3 | 56785 | 128.7 | 6.0 | 5.6 | 2.3 | 3.3 | monthly | | | P, AET/PET | Fert |
| HYBRID | 39.9 | 56785 | 128.7 | 5.7 | 7.0 | -1.6 | 8.6 | daily | P(M) | | SW | Veg-N, N |

^a A specific month is part of the growing season if its NPP estimate is greater than 10% of the maximum monthly NPP estimate of the grid cell. ^b NPP estimates are based on the assumption that the world is either covered with potential (P) or actual (A) vegetation. Vegetation type may be either an input variable, implicit within the model (e.g. NDVI data only represents actual vegetation), or explicitly simulated by the model. Within a grid cell, the vegetation may be assumed to be represented by a single dominant (D) vegetation type or a mosaic of vegetation case. In the latter case, the model uses either an average parameterization that is biome-dependent (B), or a distinct parameterization for each vegetation type (M). ^c The effect of soil moisture on NPP is described using either precipitation (Prec), soil water (i.e. soil moisture, soil water potential – SW), vapour pressure deficit (VPD), or actual evapotranspiration (AET) and potential evapotranspiration (PET). ^d Nutrient constraints are implemented based on a soil fertility factor (Fert), on the carbon and nitrogen content of soil organic matter (Soil C & N), on the nitrogen content of leaves (Leaf-N), the nitrogen content of both leaves and roots (Veg-N), and/or on inorganic nitrogen (N), phosphorus (P), or sulphur (S) concentrations in the soil. ^e N/A: not applicable because DOLY estimates only annual NPP

FASIR-based results of GLO-PEM used here are neither the optimal nor do they correspond to the published values. The results of TURC are also different from the published ones, because its calibration to the FASIR data could not be adjusted in time for the workshop. The results available for SDBM are based on another satellite data set, as well as another radiation data set—they are therefore used only for the papers focusing on light interception/light use efficiency (Ruimy *et al.* 1999) and seasonality (Bondeau *et al.* 1999).

The FASIR satellite data we used correspond to observations from 1987, while the climate data used are the 1931–60 long-term means (exception for GLO-PEM and SIB2). The years from 1931 to 1960 differed climatically from present long-term means (Hulme 1992) and probably also from 1987. The impact of this inconsistency on global NPP is probably limited, but the diagnostic values from simulations combining satellite derived vegetation activity and climate from different periods must be treated cautiously.

Among the data sets that could *not* be standardized for the intercomparison were average humidity and wind speed, which were required by some models. Vegetation distribution is an input to several models, and the selected maps (or models) affect results both at the levels of model calibration and application—a strict standardization would have removed features that are critical for the individual model design. Furthermore, the models that estimate both fluxes and vegetation structure (BIOME3, DOLY, HYBRID) do not predict identical vegetation distributions. Practically all soils data came from the FAO Soil Map of the World (FAO/UNESCO 1974), but the interpretations of its categories in terms of soil factors cannot be standardized across models easily. Some models use the translation of the Zöbler (1986) soil texture to field capacity and wilting point. Pan *et al.* (1996) recently explored the sensitivity of biosphere models to such different soil data sets.

Table 4 lists the input requirements of all models. Only input driving variables used to extrapolate simulations across the globe are listed, other variables required at an early stage in the calibration procedure are not mentioned. For example, FBM and PLAI use aggregated ecosystem types (Fung *et al.* 1987) to compute the heterotrophic respiration. The calibration procedure of these models implies that annual NPP equals annual R_H —therefore NPP cannot be estimated without such a data set. Another example are the NDVI time-series data (Gallo 1992) used by SILVAN to calibrate the phenological submodel applied for temperate deciduous forests.

The land area considered for the comparison included all major land masses except Antarctica. When the data from different sources and different spatial resolution is applied to this land mask at 0.5° longitude/latitude, then the terrestrial boundaries do not match precisely. After selection of only those cells that had data for all variables,

56 785 grid cells were left for the standardized input files (from 62 483 grid cells in CLIMATE, 58 440 for soil texture, 86 624 for the FASIR-NDVI). Model outputs covered still fewer numbers of cells for some models (Table 5). This is due to:

- 1 the use of additional data by these models;
- 2 some models do not simulate fluxes in certain vegetation types (deserts in FBM, wetlands in TEM); and
- 3 the different spatial resolution of SIB2.

In the most extreme case (FBM), the effective total land area is 18% less than the $128.7 \times 10^6 \text{ km}^2$ of the 56 785 grid cells of the common input data sets. In the accompanying papers, the number of models which could be used for the comparison, differs for various reasons explained there.

Results

In this overview, we present only results concerning global annual and seasonal NPP. In the companion papers, the following features are investigated in greater detail: the spatial pattern of annual and seasonal NPP across the globe (Kicklighter *et al.* 1999), the relationship between NPP and its major climatic drivers (Schloss *et al.* 1999), the influence of different water balance formulations on NPP (Churkina *et al.* 1999), the influence of different seasonality formulations on NPP and LAI (Bondeau *et al.* 1999), the implications of different formulations of light absorption and light use efficiency (Ruimy *et al.* 1999), and the comparison of simulated net ecosystem productivities with atmospheric CO_2 measurements (Nemry *et al.* 1999).

Annual NPP

The models estimate global annual net primary production on land between 39.9 and 80.5 Pg C with a mean of 54.9 Pg C (Table 5). The differences in total land area mentioned above do not appear to have a major influence on global NPP estimates, mainly because they concern regions with low productivity. As indicated before, the TURC simulations for Potsdam NPP Model Intercomparison were made with the FASIR NDVI data set without re-calibration, resulting in an overestimation of NPP, as well as an unrealistically long growing season (for details, see Bondeau *et al.* 1999; Ruimy *et al.* 1999) compared to published results ($62.3 \text{ Pg C year}^{-1}$ for the reference computation, Ruimy *et al.* 1996a). The low global NPP for HYBRID is probably influenced by the fact that a preindustrial atmospheric CO_2 of 280 ppmv (A. Friend, personal communication) was used, whereas all other simulations were made with atmospheric CO_2 concentrations between 340 and 360 ppmv (Table 4).

If TURC and HYBRID are left aside, then the range of variation of the global results is $\approx 50\%$ of the smallest value, which must be considered a relatively good agreement for the estimation of this poorly understood

variable. The calibration procedures used for some models are certainly partly responsible for this agreement: in fact, Ruimy *et al.* (1999) suggest that most models may be calibrated so that annual global NPP are within 'commonly admitted values'. Table 5 shows that the ranking of global NPP cannot be explained by the main model features described below, and certainly not by the basic model categories in Table 2. Satellite-based models may estimate high (TURC, GLO-PEM)³ or low global NPP (CASA, SIB2), but all of them estimate low APAR (Ruimy *et al.* 1999). The three models that do not estimate GPP (CASA, CENTURY, HRBM) produce intermediate to low values of NPP. Four of the six models that apply nutrient constraints estimate lower global NPP than all other models. Four of the six models that use vapour pressure deficit estimated higher global NPP than those using other approaches to describe the influence of moisture on NPP. This shows that NPP estimates are sensitive to the modelling strategy for the effect of water stress on NPP (Churkina *et al.* 1999). One of the two models using vapour pressure deficit that predicted a lower global NPP (DOLY) also used nutrient constraints on NPP.

Figure 1 shows the global map of annual NPP, averaged across all models. The coefficient of variance (Fig. 2b) is less than 15% for most areas—we therefore consider the broad features of this map as a comprehensive representation of NPP fluxes estimated similarly by different models. The highest annual production ($> 1000 \text{ g C m}^{-2}$) is found in the humid tropics (Amazonia, Central Africa, South-east Asia), where both temperature and moisture requirements are fully satisfied for photosynthesis. Temperate regions have an intermediate NPP ($500\text{--}700 \text{ g C m}^{-2}$), and the lowest NPP ($< 200 \text{ g C m}^{-2}$) is found in cold or arid regions, where either temperature or precipitation are limiting. Central Africa shows the highest spatial variability, from the most productive biomes (tropical evergreen forest) near the equator to the least productive ones (arid shrublands) around latitudes $20\text{--}25^\circ$.

The variation in NPP among models reflects the distribution of NPP. The standard deviation of individual model estimates from the mean (Fig. 2a) is large where NPP is high and small where NPP is low. The highest standard deviation occurs at the borders of highly productive vegetation types. This may partially be due to the different vegetation data sets (with different boundaries near ecotones) which are used as input (Bondeau *et al.* 1999). In tropical and boreal forests, the coefficient of variance is less than 5%.

Seasonal variation in global NPP⁴

Because most of the world's ice-free land area is located in the northern hemisphere (74%), the monthly

global NPP estimates of all models are low during the northern hemisphere's winter and high during its summer, but the seasonal pattern and magnitude vary among models (Fig. 3). Most models estimate the lowest global NPP in February (CARAIB, CASA and TURC in January, HYBRID in December). The lowest monthly global NPP ranges from $-1.6 \text{ Pg C month}^{-1}$ (HYBRID) to $4.8 \text{ Pg C month}^{-1}$ (TURC). All models estimate the highest monthly global NPP during the northern summer (apart from CENTURY which estimates the peak to occur in September due to a particular artefact in this simulation, which has subsequently been removed; W. Parton, personal communication). The highest monthly global NPP ranges from $5.6 \text{ Pg C month}^{-1}$ (HRBM) to $9.1 \text{ Pg C month}^{-1}$ (KGBM and TURC). The seasonal NPP variations of HYBRID ($8.6 \text{ Pg C month}^{-1}$) are more than three times larger than the seasonal variations of CASA ($2.7 \text{ Pg C month}^{-1}$). The relative intensity of the growing season is stronger in models using daily time steps than in monthly models. Models that use vapour pressure deficit (VPD) or soil moisture (SW) also estimate larger seasonal ranges in global NPP than those that use monthly precipitation, AET or potential evapotranspiration (PET). Many of the 'daily' models use variations of the Penman–Monteith algorithm to describe the influence of moisture on NPP (Churkina *et al.* 1999). It appears as if the use of different algorithms to describe the effect of moisture on NPP by the various models affects the amplitude of the seasonal variations.

Although NPP is seasonal in tropical and subtropical regions, seasonal variations of global NPP appear to be mostly influenced by seasonal NPP in boreal regions. Most models estimate higher NPP in boreal forests than in tropical evergreen forests during June, July and August. This is a result, in part, of the longer day lengths experienced by boreal forests during the summer in the northern hemisphere (cf. Kicklighter *et al.* 1999).

Conclusions

This first systematic comparison of terrestrial biogeochemical models, using a primary output connected to a range of ecosystem processes (NPP), demonstrates agreement between the present generation of models for many broad features of the overall behaviour, despite the fact that the models were developed for widely differing purposes and with widely differing resource

⁴ With the exception of the DOLY model, the participants had provided spatially explicit NPP estimates on a monthly basis so that differences in seasonal NPP estimates among the models could be examined in addition to annual NPP estimates. Therefore, seasonal NPP patterns are compared only among the remaining 15 models.

³ This holds even when the FASIR data is not used.

bases for personnel and computing power. However, and perhaps more interestingly, both the differences in model behaviour and the unresolved question of calibration to an assumed total NPP have identified important shortcomings in our understanding of the total Earth system. These need to be reduced if predictions or sensitivity assessments of the stability and sustainability of the terrestrial biosphere, are demanded. Better predictions cannot come from improved physical models of the ocean and the atmosphere alone, even if these are needed as well. Most recent assessments (e.g. Melillo *et al.* 1996) highlight evidence that the coupled Earth System is highly sensitive to the dynamics of the biosphere.

Recently, new technological and scientific developments have indicated that our ability to observe changes in biospheric activity may be greater than anticipated: Keeling *et al.* (1996) suggested that, at least since 1960, biospheric activity in northern latitudes may have changed strongly enough to produce an average extension of the growing period by seven days, and Myneni *et al.* (1997) used the AVHRR satellite record to confirm this result, while also indicating the regional uncertainties. The modelling teams aiming at simulating global carbon fluxes now face the challenge to explain or reject these and other hypotheses about the dynamics of the Earth's vegetation.

This will clearly call for the development of new modelling approaches. Nevertheless, the potential of the current philosophy has in no way been exhausted. Model comparisons play an important role for the development of the science. Numerous 'minor findings' from the working group discussions have already led to improved versions of the models. In several cases, the thorough scrutiny provided by colleagues during the comparison process helped identify errors or inadequacies that have subsequently been rectified.

Further improvements must come from better exploiting the potential of observations. Several lines for this are now clear:

- 1 consolidation of existing data sets on flux integrals such as GPPDI, using a broad range of NPP measurements;
- 2 connection of model tests to measurement networks such EUROFLUX and Ameriflux;
- 3 use of better remote sensing products through the development of techniques for the new sensors becoming available and through improved processing of previous data sets such as the AVHRR archives.

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