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► To cite this version:

D. Kicklighter, Alberte Bondeau, A. Schloss, J. Kaduk, A. David Mcguire, et al.. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology*, 1999, 5 (S1), pp.1-15. 10.1046/j.1365-2486.1999.00009.x . hal-01757668

HAL Id: hal-01757668

<https://hal.science/hal-01757668>

Submitted on 14 Sep 2022

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Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biomes

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INTERCOMPARISON*

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Annual and seasonal net primary productivity estimates (NPP) of 15 global models across latitudinal zones and biomes are compared. The models simulated NPP for con-temporary climate using common, spatially explicit data sets for climate, soil texture, and normalized difference vegetation index (NDVI). Differences among NPP estimates varied over space and time. The largest differences occur during the summer months in boreal forests (50° to 60°N) and during the dry seasons of tropical evergreen forests. Differences in NPP estimates are related to model assumptions about vegetation structure, model parameterizations, and input data sets.

Keywords: NPP, seasonal, global, model, boreal forest, tropical forest

Introduction

Because environmental conditions change over the earth's surface, net primary productivity (NPP) of terrestrial vegetation varies over space and time. To account for the spatial variations in NPP across the globe, all models in the Potsdam NPP Model Intercomparison activity (Cramer *et al.* 1999) developed spatially referenced NPP estimates with a resolution of 0.5° latitude × 0.5° longitude. In addition, most of the models developed these spatially referenced estimates at a daily or monthly resolution. By comparing spatial and seasonal variations of NPP among the models, it should be possible to pinpoint regions and/or times where differences in model assumptions cause large variations

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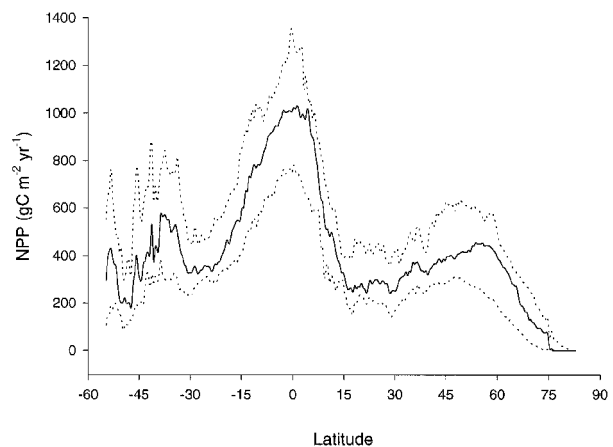


Fig. 1 Comparison of the latitudinal distribution of the median (solid line), and 10th and 90th percentiles (dotted lines) of area-weighted mean annual net primary productivity estimated by 15 models within a 0.5° latitudinal band.

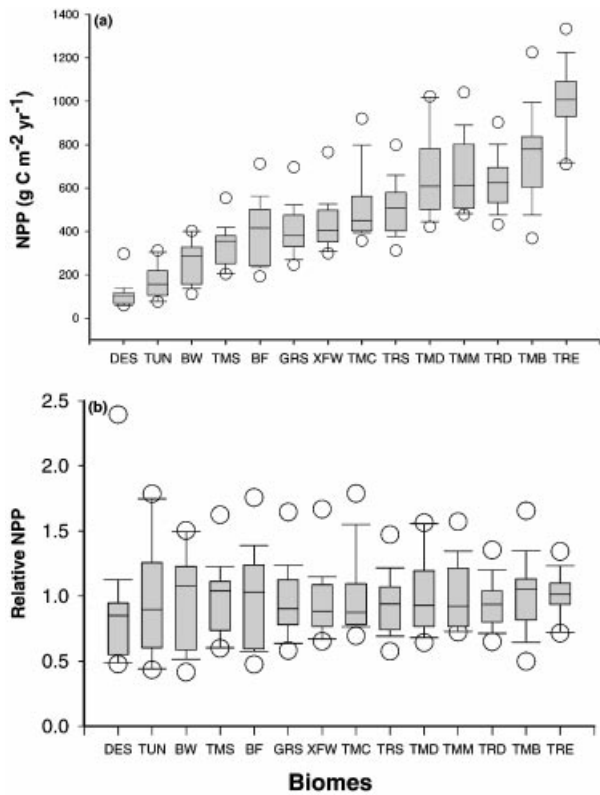


Fig. 2 Box plots comparing the variability in model estimates among biomes for (a) annual net primary productivity and (b) annual net primary productivity relative to mean annual net primary productivity estimated from the combined model results (i.e. grid cell NPP estimated as the average of all model NPP estimates; see Cramer *et al.* 1999). Biomes include arid shrublands/deserts (DES), tundra (TUN), boreal woodlands (BW), temperate savannas (TMS), boreal forest (BF), grasslands (GRS), xeromorphic woodlands (XFW), temperate conifer forests (TMC), tropical savannas (TRS), temperate deciduous forests (TMD), temperate mixed forests (TMM), tropical deciduous forests (TRD), temperate broad-leaved evergreen forests (TMB) and tropical evergreen forests (TRE). Biomes are arranged in ascending order of the mean biome NPP estimated from the combined model results. Bars within the boxes represent median values. The bottom and top of the box represents the 25th and 75th percentile, respectively. The bars outside the box represent the 10th and 90th percentiles. Open circles represent outliers.

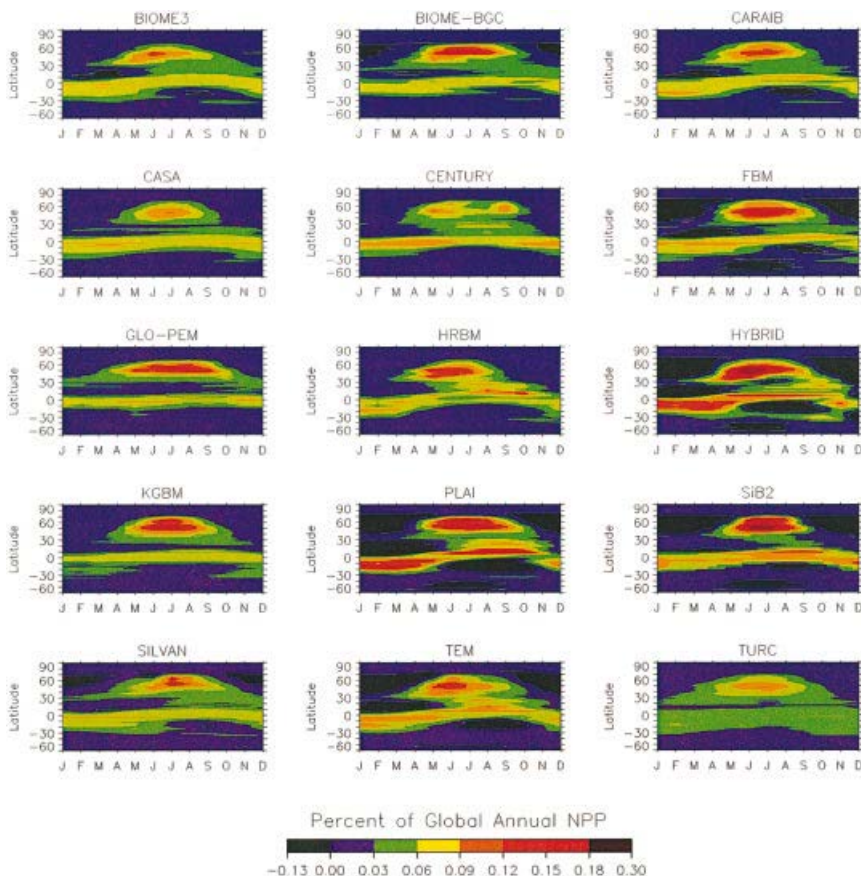


Fig. 3 Comparison among models of the relative distribution (percentage) of global annual NPP across latitudes and months.

in NPP estimates. This can provide a starting point for identifying issues that cause the global NPP estimates of these models to vary by a factor of two (39.9–80.5 Pg C year⁻¹; see Cramer *et al.* 1999). With these insights, focused studies can then be developed to help resolve these discrepancies in future NPP estimates and improve our understanding of terrestrial productivity.

Materials and methods

Fifteen models of the Potsdam NPP Model Intercomparison activity, described in Cramer *et al.* (1999), provided spatially referenced NPP estimates with a monthly temporal resolution: BIOME3, BIOME-BGC, CARAIB, CASA, CENTURY, FBM, GLO-PEM, HRBM, HYBRID, KGBM, PLAI, SIB2, SILVAN, TEM and TURC. To examine the spatial patterns of NPP estimated across the globe, we compared area-weighted means of annual NPP estimates (i.e. areal NPP) averaged across longitudes in 0.5° latitudinal bands. We also compared area-weighted means of annual NPP estimates averaged across biomes as delimited by a modified version of the potential vegetation map given in Melillo *et al.* (1993). Although the models used different vegetation maps with different classification schemes to develop the NPP estimates in the Potsdam NPP Model Intercomparison, we used the Melillo *et al.* (1993) data set to provide a common mask in order to examine regional differences in NPP among the models. The model comparisons presented in this paper are based on the 56 785 ‘common’ grid cells for which all models provided output data.

To compare seasonal patterns of NPP, NPP was first summed across all land areas in each 0.5° latitudinal band (60°S to 90°N) during a single month and this value was divided by the global annual NPP estimate of the same model (cf. Cramer *et al.* 1999). We then took a closer look at seasonal variations in boreal forests and tropical evergreen forests by comparing mean monthly NPP, averaged by biome, among the models.

Results

Comparison of spatial variations in simulated annual NPP

The models estimate a trimodal distribution of annual NPP across a latitudinal gradient (Fig. 1) with the highest areal NPP occurring around the equator 5°S to 5°N; a second, smaller peak in NPP occurring between 35° and 45°S; and a third, smaller peak occurring between 50° and 60°N. Within these general trends, the magnitude of annual NPP estimated by the models varies considerably, especially around the three latitudinal peaks of NPP, but no model estimates consistently higher or lower NPP across all latitudes.

The NPP estimates of all models generally increase from cold, dry biomes to warm, moist biomes (Fig. 2a). Most models estimate that the grid cells grouped as tropical evergreen forests have the highest NPP among all biomes, followed by temperate broad-leaved evergreen forests. In contrast, arid shrublands/deserts are the least productive biomes among the models. Most models also estimate that tundra and boreal woodlands have low productivity. In other biomes, the relative order of mean biome NPP varies among the models. The ranking of mean biome NPP for tropical savannahs varies the most among the models. The SIB2 model estimates tropical savannahs to be the second most productive biome, whereas the GLO-PEM model estimates tropical savannahs to be the tenth most productive of the 14 biomes considered in this study. In corresponding latitudinal zones (i.e. boreal, temperate, and tropical), forests have higher mean biome NPP than savannahs, grasslands, or shrublands, but grid cells grouped as grasslands in this study have a higher mean biome NPP than grid cells grouped as temperate savannahs for most models.

The greatest range in mean biome NPP among the models occurs in the productive temperate broad-leaved evergreen forests, but considerable variability among mean biome NPP estimates (as indicated by the large intervals between the 25th and 75th percentiles in Fig. 2a) also occurs in temperate mixed forests, temperate deciduous forests, and boreal forests. Mean biome NPP estimates for tundra have the smallest range, but mean biome NPP estimates appear to be the most similar for arid shrublands/deserts. Biomes in the boreal region (i.e. tundra, boreal woodlands, boreal forests) have the greatest relative difference in mean biome NPP estimates (Fig. 2b) whereas tropical evergreen forests have the smallest relative differences.

Comparison of seasonal NPP

Net primary productivity varies seasonally across all latitudes (Fig. 3) for all models. Over half of the models (BIOME3, BIOME-BGC, CARAIB, FBM, HYBRID, PLAI, SIB2, SILVAN, TEM) estimate a negative NPP for some latitudinal bands during some part of the year. A negative NPP indicates that plant respiration is greater than the uptake of carbon by plants during a month. For most models, the seasonal changes of NPP are greater in the northern temperate and boreal regions than in tropical regions such that all models estimate that more NPP occurs in northern temperate and boreal regions during some part of the northern hemisphere summer. However, most models also simulate a longer growing season in tropical and subtropical regions so that annual NPP estimates are higher in these regions.

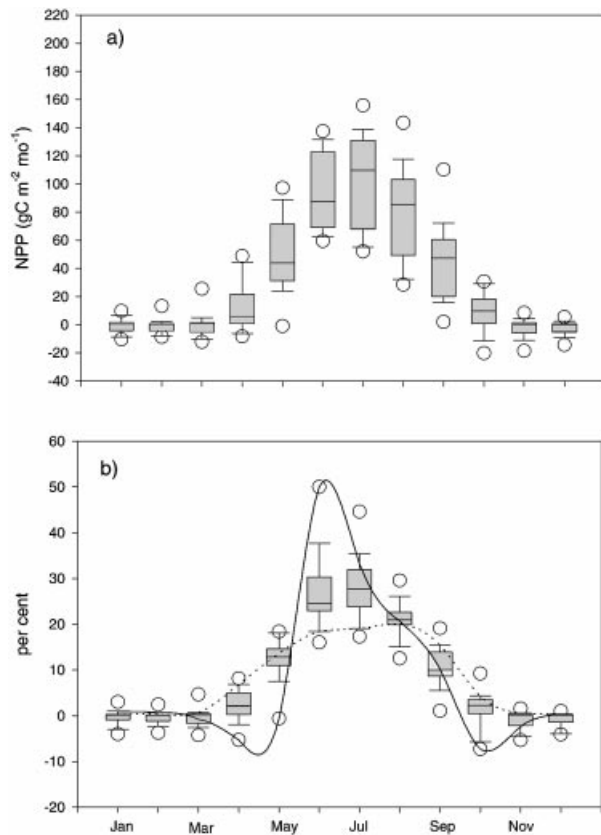


Fig. 4 Box plots comparing the seasonal patterns of model estimates in boreal forests for (a) monthly NPP estimates and (b) relative seasonal distribution of annual NPP. Bars within the boxes represent median values. The bottom and top of the box represents the 25th and 75th percentile, respectively. The bars outside the box represent the 10th and 90th percentiles. Open circles represent outliers. The relative seasonal distribution of annual NPP estimated by TEM (solid line) and GLO-PEM (dotted line) are presented to highlight differences in the width and breadth of the summer NPP peak estimated by the models.

In the northern temperate and boreal regions, NPP is relatively high from May to August with the greatest range in seasonal NPP occurring between 45° and 60°N for most models. Although seasonal trends are similar, the proportion of global NPP represented by the summer NPP peak varies among the models, indicating differences in assumptions about the relative importance of northern temperate and boreal regions on global NPP. The proportion of global NPP represented by the summer NPP peak is relatively low for CASA, CENTURY and TURC, but high for HYBRID and SIB2.

Differences in NPP estimates at finer spatial and temporal resolutions among the models are not necessarily reflected in comparable global NPP estimates. For example, the CASA and PLAII models estimate a similar global NPP of about 49Pg C year^{-1} (cf. Cramer *et al.* 1999), but this global NPP is distributed very differently

over space and time between the two models (Fig. 3). Large seasonal variations in NPP are estimated by PLAII such that intense productivity (up to 0.20% of annual global NPP in a single month) occurs in a 0.5° latitudinal band during the growing season. This intense productivity compensates for large respiratory losses of carbon (up to 0.11% of annual global NPP in a single month) during dormant periods. In contrast, CASA estimates a smaller range in seasonal NPP (between 0.00 and 0.13% of annual global NPP) such that annual global NPP is distributed more evenly over space and time.

The northern temperate/boreal latitudinal band (i.e. 50°N to 60°N) is covered predominantly by boreal forests (51%) whereas the tropical latitudinal band (i.e. 5°S to 5°N) is covered predominantly by tropical evergreen forests (78%). Therefore, the variations in annual and seasonal NPP at these latitudes are most likely a result of differences in how the models simulate NPP in these biomes. Variations in areal NPP in the southern temperate latitudinal band (35° to 45°S) are related to differences in how the models simulate NPP in temperate broad-leaved evergreen forests, xeromorphic woodlands, temperate savannahs, grasslands and deserts. However, no biome dominates the vegetation cover in this latitudinal band and a very small proportion of annual global NPP occurs in this latitudinal band (Fig. 3). Therefore, we focus further comparisons on seasonal NPP estimates in boreal forests and tropical evergreen forests.

Seasonal estimates of NPP in boreal forests. As indicated by the seasonal patterns of the northern temperate/boreal latitudinal band (Fig. 3), NPP in boreal forests is high from June to August and low from November to March for all models (Fig. 4a). Differences in monthly NPP estimates among the models also vary seasonally. The largest differences occur during summer ($114.9\text{gC m}^{-2} \text{month}^{-1}$ in August) when all models estimate high NPP. The model estimates are the most similar during the winter months (within $20.1\text{gC m}^{-2} \text{month}^{-1}$ in January) when primary productivity is considered to be low or non-existent. These differences are due to variations in both the timing and magnitude of NPP estimated by the models.

Most models estimate the highest NPP in July, which is the month with the highest temperatures and precipitation (cf. Schloss *et al.* 1999) at these latitudes. However, CENTURY, HYBRID, PLAII and TEM estimate the highest NPP in June which is the month with the highest inputs of solar radiation (cf. Schloss *et al.* 1999). Besides timing, the models also differ on the relative size and breadth of the summer NPP peak. For example, TEM assumes a relatively narrow, but large peak of NPP with almost half of the annual NPP occurring in June (Fig. 4b). In contrast, GLO-PEM assumes a wide, but lower peak of

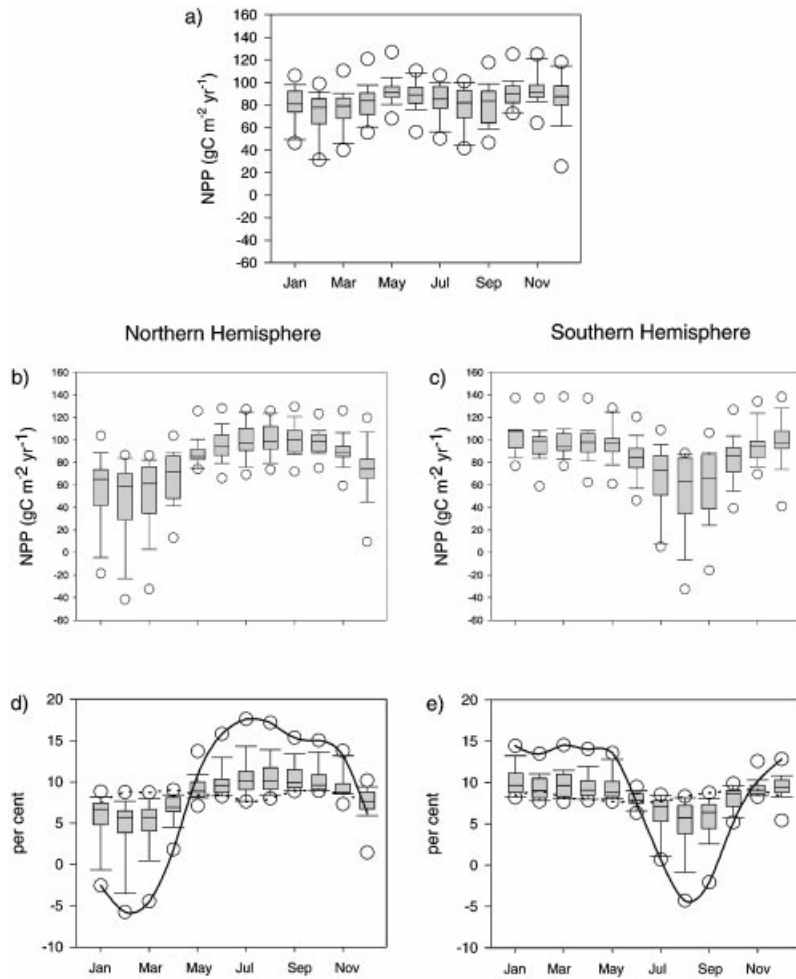


Fig. 5 Box plots comparing the seasonal patterns of model estimates for (a) mean monthly NPP estimates for all tropical evergreen forests; (b) mean monthly NPP estimates for tropical evergreen forests in the northern hemisphere; (c) mean monthly NPP estimates for tropical evergreen forests in the southern hemisphere; (d) relative seasonal distribution of annual NPP in tropical evergreen forests of the northern hemisphere; and (e) relative seasonal distribution of annual NPP in tropical evergreen forests of the southern hemisphere. Bars within the boxes represent median values. The bottom and top of the box represents the 25th and 75th percentile, respectively. The bars outside the box represent the 10th and 90th percentiles. Open circles represent outliers. The relative seasonal distribution of annual NPP estimated by PLAI (solid line) and TURC (dotted line) are presented to highlight differences in relative seasonal variations of NPP assumed by the models.

NPP with about 20% of annual NPP occurring in each month from June to August. As a result of these differences, the relative seasonal distribution of annual NPP varies the most among the models in June and July. In August, the variations in NPP estimates are due mainly to differences in the assumed magnitude of NPP in boreal forests because the relative proportion of annual NPP is similar (about 20%) among the models.

Seasonal NPP in tropical evergreen forests. In contrast to the seasonal patterns of NPP within the tropical latitudinal band (Fig. 3), mean biome NPP simulated by most models for tropical evergreen forests is fairly constant over the year (Fig. 5a). Most of this discrepancy can be accounted for if seasonal NPP of tropical evergreen forests in the northern hemisphere are examined separately from those in the southern hemisphere. Net primary productivity in northern tropical evergreen forests is relatively high from June to October and relatively low from December to April (Fig. 5b). In contrast, NPP is relatively high from December to May and relatively low from July to

September in southern tropical evergreen forests (Fig. 5c). Thus, the different seasonal patterns of NPP in tropical evergreen forests in the northern and southern hemispheres compensate each other when examining seasonal patterns of NPP at the biome scale. The seasonal patterns of NPP in the northern and southern tropical evergreen forests correspond to seasonal variations in precipitation and solar radiation (cf. Schloss *et al.* 1999) around the equator.

Differences in monthly NPP estimates among the models also vary seasonally in tropical evergreen forests of the northern and southern hemispheres. The largest differences occur during the dry season in both hemispheres (up to $128.4 \text{ g C m}^{-2} \text{ month}^{-1}$ in February for northern forests and $122.1 \text{ g C m}^{-2} \text{ month}^{-1}$ in September for southern forests) when NPP estimates are relatively low. The model estimates are the most similar during the wet season when NPP estimates are relatively high. Again, these differences are due to variations in both the timing and magnitude of NPP estimated by the models. For example, TURC assumes very little seasonality of NPP

in tropical evergreen forests in the northern or the southern hemisphere such that annual NPP is divided approximately equally across all months (Fig. 5d,e). In contrast, PLAI assumes much larger seasonal variation in NPP in northern and southern forests such that NPP during the wet season compensates for the loss of carbon due to respiration (up to 6% of annual NPP per month) during the dry season. However, the variability in the relative proportion of annual NPP occurring each month, as represented by the interval between the 25th and 75th percentiles in Fig. 5(d,e), is similar between the wet and dry seasons indicating that variations in monthly NPP are also due to differences in the assumed magnitude of NPP by the models.

Discussion

These models use several approaches to generate spatial and temporal variations in NPP. Each approach is based on simplifying assumptions about how ecosystems are structured and how vegetation may respond to changes in various environmental factors. As each approach is imperfect, NPP estimates are biased by the formulations and/or parameter values used by the models to develop them. For example, the formulations used in the models that calculate NPP directly (HRBM, CASA, CENTURY) will never estimate a negative NPP. Positive annual NPP estimates are calculated in HRBM based on monotonic relationships with temperature and precipitation from a minimum annual NPP estimate of zero. This annual NPP is then distributed monthly based on a ratio of monthly actual evapotranspiration to annual evapotranspiration. In CASA, monthly NPP estimates are never negative because monthly incident photosynthetically active radiation (PAR), the fraction of PAR intercepted by the canopy (FPAR) or light use efficiency (LUE) never fall below zero. In CENTURY, a maximum potential monthly NPP is reduced based on environmental scaling factors to a minimum of zero. In contrast, the models that calculate NPP as the difference between gross primary productivity (GPP) and autotrophic respiration (R_A) can calculate a negative NPP in months when R_A is larger than GPP.

Below, we examine how the NPP estimates of the models in this study are influenced by: (1) differences in model assumptions about vegetation structure and sensitivities to environmental factors; (2) model parameterization; (3) input data; and (4) land use.

Importance of vegetation structure on NPP estimates

Differences in the assumed structure of vegetation among the models influence the calculation of seasonal NPP from GPP and R_A . In TEM, variations of vegetation structure and environmental conditions within the

canopy are ignored so that the model simulates GPP and R_A of vegetation as a single entity based on parameters calibrated to field data. Seasonal variations in canopy structure are determined implicitly with the input variable KLEAF. In contrast, BIOME3, CARAIB, HYBRID, SIB2 and SILVAN simulate carbon dynamics of individual leaf layers of the canopy, based on extensions of the leaf photosynthesis model of Farquhar *et al.* (1980), and then scale these leaf level carbon dynamics to the canopy level by accounting for variations in structure and environmental conditions within the canopy (cf. Sellers *et al.* 1992). Unlike TEM, these models also simulate seasonal changes in canopy structure, but the simulated canopy dynamics may be very different among the models (Bondeau *et al.* 1999). Thus, GPP is calculated from leaf photosynthesis and R_A is calculated from leaf, root and stem respiration after the appropriate allocation of carbon to these vegetation compartments. The calculation of GPP and NPP in the 'leaf' models also tends to occur at finer temporal resolutions than TEM. The relatively large seasonal variations of NPP estimated by HYBRID and SIB2 may be a result of simulating canopy dynamics with a leaf photosynthesis model and calculating NPP with a daily or finer time-step rather than a monthly time-step. However, the relative seasonal variations of NPP estimated by BIOME3, CARAIB and SILVAN are similar to those estimated by TEM.

Importance of environmental factors on NPP estimates

Differences in assumed sensitivities to temperature, moisture, solar radiation (Churkina *et al.* 1999; Ruimy *et al.* 1999; Schloss *et al.* 1999) and nutrient constraints (Schimel *et al.* 1997; Pan *et al.* 1998) also cause seasonal variations of NPP to differ among the models. The large differences in NPP estimates of boreal forests during June and July are related to differences in the sensitivity of simulated NPP to temperatures among the models during this period (cf. Schloss *et al.* 1999). These different sensitivities result from various assumptions about the relationships among temperature, soil temperature, snow pack, permafrost and NPP among the models. The large differences in NPP estimates of tropical evergreen forests during the dry seasons are related to different sensitivities to precipitation and solar radiation during these periods (cf. Schloss *et al.* 1999). These different sensitivities result from assumptions about the influence of moisture on NPP and the general availability of moisture throughout the year (cf. Churkina *et al.* 1999). Future studies that improve our understanding of the effects of frozen and thawing soils on NPP in boreal forests and the effect of deep roots in tropical evergreen forests would help to reduce the uncertainty associated with developing global NPP estimates.

Importance of model parameterization on NPP estimates

Although PLAI uses the same functional formulations as FBM, the seasonal and latitudinal distribution of NPP estimated by PLAI is different from FBM. To simulate the effects of climate change on both ecosystem structure and function, PLAI was developed to couple the BIOME (Prentice *et al.* 1992) model to FBM, but the model uses a different parameterization than FBM because the vegetation classification scheme used by BIOME is different from that used in the Matthews (1983) vegetation data set normally used by FBM. Thus, the differences between the NPP estimates of FBM and PLAI are a result of differences in parameterization of the FBM formulations and differences in the vegetation distribution described by the two vegetation data sets.

Importance of input data on NPP estimates

As the FPAR formulations in CASA and TURC depend on the input of seasonal NDVI data, the relatively constant monthly NPP estimated by these models in the tropics is partly explained by the weak seasonality of the FASIR-NDVI data set (Bondeau *et al.* 1999; Schloss *et al.* 1999) used by these models. Although NDVI of tropical evergreen forests are assumed to be constant over the year in the FASIR-NDVI data set (Sellers *et al.* 1994), other modelling studies using other NDVI data sets (Knorr & Heimann 1995; Heimann *et al.* 1998) have also indicated a weak seasonality of NPP in the tropics. The weak seasonality of the NDVI data in the tropics suggests that the seasonal drought conditions may not be as pronounced as indicated by most of the NPP models. Nepstad *et al.* (1994) have observed that tropical trees can have roots down to soil depths greater than 8 m so that evergreen forests have been able to maintain evapotranspiration during 5-month dry periods by accessing deep soil water. Most of the NPP models in this intercomparison have rooting zones for tropical forests that range from 1 to 3 m (Churkina *et al.* 1999) so that vegetation never would have access to the deep water in the model simulations and would undergo drought stress. The use of NDVI by the CASA and TURC models may implicitly account for the effects of deep rooting on phenology, but other models that use NDVI data (e.g. GLO-PEM, SIB2) still show a pronounced seasonality in the tropics.

Importance of land use on NPP estimates

In this study, most models estimate NPP assuming the world is covered by potential vegetation (Cramer *et al.* 1999). Three models (CARAIB, CASA, SIB2) estimate NPP assuming the world is covered with actual vegetation, i.e. including human land use. TURC uses potential vegetation to help define the spatial distribution of biomass but

also uses NDVI data, which implicitly assumes the world is covered with actual vegetation, to describe seasonal canopy characteristics. GLO-PEM does not use a vegetation data set either, but uses satellite data to describe seasonal changes in temperature, vapour pressure deficit, soil moisture and absorbed photosynthetically active radiation that influence seasonal canopy characteristics. As land use is considered to be the most important determinant of carbon storage, uptake, and release from the terrestrial biosphere (Sampson *et al.* 1993), some of the variability observed among the model NPP estimates might be caused by the consideration of land use by various models. The conversion of forests to agriculture is generally assumed to decrease productivity (Aselmann & Lieth 1983; Houghton *et al.* 1983), but irrigation practices may actually enhance NPP in arid regions. A comparison of the actual vegetation data set of Loveland & Belward (1997) to the potential vegetation data set of Melillo *et al.* (1993) indicates that agriculture has affected some biomes more than other biomes. Over 40% of the area designated as temperate mixed forests, temperate deciduous forests and tropical deciduous forests; and 30% of temperate savannahs and temperate broad-leaved evergreen forests have been affected by agriculture. In contrast, only about 10% of boreal forests and 15% of tropical evergreen forests have been affected by agriculture. Although the variability in NPP estimates in temperate mixed forests and temperate deciduous forests (Fig.2) may be partially related to the consideration of land use by some models, no clear trend of the effect of land use is evident among the models at the global and biome scales. Overall, the uncertainty of NPP estimates caused by differences in model conceptualization is apparently much greater than variation in NPP caused by the consideration of land use.

Assessment of seasonal NPP estimates

Most field measurements of NPP that are available for developing and checking models have a temporal resolution of a few months (i.e. the growing season) to a year because NPP has usually been determined as the accumulation of biomass over a specified time. Thus, the daily and monthly NPP estimates developed by the models in this study are more temporally resolved than currently available field data so we must rely on inferences from other sources of information to determine if model estimates of seasonal NPP are reasonable. The availability of field measurements of carbon fluxes at finer temporal resolutions (hour, day or month), such as gross ecosystem exchange (GEE) and net ecosystem exchange (NEE) determined by eddy covariance techniques (e.g. Wofsy *et al.* 1988, 1993; Fan *et al.* 1990; Gao 1994; Grace *et al.* 1995, 1996; Baldocchi *et al.* 1996; Black *et al.* 1996; Goulden *et al.* 1996; Greco & Baldocchi 1996; Valentini *et al.* 1996),

would help modelling groups to constrain their estimates of seasonal GPP and net ecosystem production (cf. Ruimy *et al.* 1996; Goulden *et al.* 1998) and lead to a reduction in the uncertainty of NPP estimates among the models. Although the eddy covariance studies provide additional information about seasonal changes in carbon fluxes, these field measurements still occur at a fine spatial scale such that evaluation of model estimates are limited by the heterogeneity of environmental conditions in a grid cell (cf. Cramer *et al.* 1999).

Satellite data, on the other hand, provides seasonal information over large scales. The comparison of seasonal estimates of intermediate variables determined by the models (e.g. FPAR) to satellite data (Rignot & Way 1994; Way *et al.* 1994; Knorr & Heimann 1995; Fischer *et al.* 1996; Bondeau *et al.* 1999) provides additional checks to evaluate seasonal NPP estimates even if the satellite data cannot be compared to NPP directly.

Seasonal data from a comprehensive monitoring network of atmospheric CO₂ concentrations (Conway *et al.* 1994a,b) provide another source of information to evaluate the large-scale carbon dynamics of NPP models. Latitudinal trends in seasonal atmospheric CO₂ measurements may be compared to simulated CO₂ concentrations developed from seasonal patterns of net ecosystem production simulated by many terrestrial carbon models and the movement of air simulated by an atmospheric transport model (Nemry *et al.* 1996, 1999; Heimann *et al.* 1998). Net ecosystem production (NEP) is the difference between NPP and heterotrophic respiration. Because measurements at different monitoring stations integrate seasonal CO₂ exchanges across different regions (Kaminski *et al.* 1996), the comparison of simulated CO₂ exchanges based on a particular NPP model with those from a calibrated diagnostic model, such as the Simple Diagnostic Biosphere Model (SDBM, Knorr & Heimann 1995) help to identify crucial regions from which the modelled CO₂ fluxes are not consistent with the latitudinal observations. Similar analyses conducted with seasonal changes in ¹³C/¹²C ratios (Ciais *et al.* 1995) or O₂/N₂ ratios (Bender *et al.* 1996; Keeling *et al.* 1996) may help to further constrain model estimates of seasonal carbon fluxes from terrestrial ecosystems. Although such comparisons do not strictly validate a model's NPP estimates, a consistency between these various forms of information will improve our understanding of the global carbon cycle and build confidence in future NPP estimates.

Conclusion

Our study has found many similarities and differences among 15 NPP models in the distribution of annual and

seasonal NPP across the surface of the globe. The largest differences occur during early summer in boreal/northern temperate latitudes of the northern hemisphere and during the dry seasons in tropical latitudes. A focused model comparison examining the simulated response of NPP to frozen and thawing soils during June and July in boreal forests should help resolve the large differences among NPP estimates observed in the boreal/northern temperate latitudes. A similar comparison examining the effects of deep roots during the dry seasons in tropical evergreen forests should help resolve the large differences among NPP estimates observed in the tropical latitudes.

Since only few direct measurements of seasonal NPP exist, other approaches must be used to evaluate the reasonableness of seasonal NPP estimates of simulation models. Data from eddy covariance studies, satellites, atmospheric CO₂ monitoring stations and isotope (e.g. ¹³C/¹²C) or element (O₂/N₂) ratios provide information that may be used to evaluate seasonal NPP estimates indirectly and build confidence in our ability to understand and simulate the global carbon cycle.

Acknowledgements

We thank Blandine Lurin for preparing and organizing the results from the various models to facilitate the model intercomparisons. We also thank John Helfrich and Xiangming Xiao for their assistance with the graphics. In addition, we thank J.M. Melillo, John Helfrich, Chris Field and two anonymous reviewers for useful comments on earlier drafts of the manuscript. The scientific sponsorship of this workshop was jointly by GAIM, DIS, and GCTE, and it was hosted by the Potsdam Institute of Climate Impact Research (PIK), with financial support from NASA, the European Commission and the U.S. Environmental Protection Agency.

References

- Aselmann I, Lieth H (1983) The implementation of agricultural productivity into existing global models of primary productivity. *Mitt. Geol.-Paläont. Inst. der Univ. Hamburg*, **55**, 107–118.
- Baldocchi D, Valentini R, Running S, Oechel W, Dahlman R (1996) Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biology*, **2**, 159–168.
- Bender M, Ellis T, Tans P, Francey R, Lowe D (1996) Variability in the O₂/N₂ ratio of southern hemisphere air. 1991–94: Implications for the carbon cycle. *Global Biogeochemical Cycles*, **10**, 9–21.
- Black TA, den Hartog G, Neumann HH *et al.* (1996) Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biology*, **2**, 219–229.
- Bondeau A, Kicklighter DW, Kaduk J *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. *Global Change Biology*, **5** (Suppl. 1), 35–45.
- Churkina G, Running SW, Schloss A *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): the

- importance of water availability. *Global Change Biology*, **5** (Suppl. 1), 46–55.
- Ciais P, Tans PP, Trolier M, White JWC, Francey RJ (1995) A large northern hemisphere terrestrial CO₂ sink indicated by the ¹³C/¹²C ratio of atmospheric CO₂. *Science*, **269**, 1098–1102.
- Conway TJ, Tans PP, Waterman LS (1994b) Atmospheric CO₂ from sites in the NOAA/CMDL air sampling network. In: *Trends '93: a Compendium of Data on Global Change* (eds Boden TA *et al.*), pp. 41–119. ORNL/CDIAC-65, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN.
- Conway TJ, Tans PP, Waterman LS, Thoning KW, Buanerkitzis DR, Masarie KA, Zhang N (1994a) Evidence for interannual variability of the carbon cycle from the NOAA/CMDL global air sampling network. *Journal of Geophysical Research*, **99D**, 2831–2822.
- Cramer W, Kicklighter DW, Bondeau A *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology*, **5** (Suppl. 1), 1–15.
- Fan SM, Wofsy SC, Bakwin PS, Jacob DJ, Fitzjarrald DR (1990) Atmosphere-biosphere exchange of CO₂ and O₃ in the central Amazon forest. *Journal of Geophysical Research*, **95**, 16851–16864.
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, **149**, 78–90.
- Fischer A, Louahala S, Maisongrande P, Kergoat L, Dedieu G (1996) Satellite data for monitoring, understanding and modelling of ecosystem functioning. In: *Global Change and Terrestrial Ecosystems* (eds Walker B, Steffen W), pp. 566–591. Cambridge University Press, Cambridge.
- Gao W (1994) Atmosphere-biosphere exchange flux of carbon dioxide in a tallgrass prairie modeled with satellite spectral data. *Journal of Geophysical Research*, **99**, 1317–1327.
- Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC (1996) Measurements of carbon sequestration by long-term eddy covariance: Methods and a critical evaluation of accuracy. *Global Change Biology*, **2**, 169–182.
- Goulden ML, Wofsy SC, Harden JW *et al.* (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–217.
- Grace J, Lloyd J, McIntyre J *et al.* (1995) Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia. 1992–93. *Science*, **270**, 778–780.
- Grace J, Malhi Y, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS (1996) The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forests. *Global Change Biology*, **2**, 209–217.
- Greco S, Baldocchi DD (1996) Seasonal variations of CO₂ and water vapour exchange rates over a temperate deciduous forest. *Global Change Biology*, **2**, 183–197.
- Heimann M, Esser G, Haxeltine A *et al.* (1998) Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO₂: first results of a model intercomparison study. *Global Biogeochemical Cycles*, **12**, 1–24.
- Houghton RA, Hobbie JE, Melillo JM *et al.* (1983) Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO₂ to the atmosphere. *Ecological Monographs*, **53**, 235–262.
- Kaminski T, Giering R, Heimann M (1996) Sensitivity of the seasonal cycle of CO₂ at remote monitoring stations with respect to seasonal surface exchange fluxes determined with the adjoint of an atmospheric transport model. *Physics of the Chemistry and the Earth*, **21**, 457–462.
- Keeling RF, Piper SC, Heimann M (1996) Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature*, **381**, 218–221.
- Knorr W, Heimann M (1995) Impact of drought stress and other factors on seasonal land biosphere CO₂ exchange studied through an atmospheric tracer transport model. *Tellus*, **47B**, 471–489.
- Loveland TR, Belward AS (1997) The IGBP-DIS global 1 km land-cover data set, DISCOVER-first results. *International Journal of Remote Sensing*, **18**, 3291–3295.
- Matthews E (1983) Global vegetation and land use: new high-resolution data bases for climate studies. *Journal of Climate and Applied Meteorology*, **22**, 474–487.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vörösmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.
- Nemry B, François L, Gérard J-C *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): analysis of the seasonal atmospheric CO₂ signal. *Global Change Biology*, **5** (Suppl. 1), 65–76.
- Nemry B, François L, Wamant P, Robinet F, Gérard JC (1996) The seasonality of the CO₂ exchange between the atmosphere and the land biosphere: a study with a global mechanistic vegetation model. *Journal of Geophysical Research*, **101**, 7111–7125.
- Nepstad DC, de Carvalho CR, Davidson EA *et al.* (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, **372**, 666–669.
- Pan Y, Melillo JM, McGuire AD *et al.* (1998) Modeled responses of terrestrial ecosystems to elevated atmospheric CO₂: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia*, **114**, 389–404.
- Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.
- Rignot E, Way JB (1994) Monitoring freeze–thaw cycles along north–south Alaskan transects using ERS-1 SAR. *Remote Sensing of the Environment*, **49**, 131–137.
- Ruimy A, Kergoat L, Bondeau A *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. *Global Change Biology*, **5** (Suppl. 1), 56–64.
- Ruimy A, Kergoat L, Field CB, Saugier B (1996) The use of CO₂ flux measurements in models of the global terrestrial carbon budget. *Global Change Biology*, **2**, 287–296.
- Sampson RN, Apps M, Brown S *et al.* (1993) Workshop summary statement: Terrestrial biospheric carbon fluxes – quantification of sinks and sources of CO₂. *Water, Air and Soil Pollution*, **70**, 3–15.
- Schimel DS, VEMAP Participants, Braswell BH (1997) Continental scale variability in ecosystem processes: models, data, and the role of disturbance. *Ecological Monographs*, **67**, 251–271.
- Schloss AL, Kicklighter DW, Kaduk J *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the Normalized Difference Vegetation Index. *Global Change Biology*, **5** (Suppl. 1), 25–34.
- Sellers PJ, Berry JA, Collatz GJ, Field CB, Hall FG (1992) Canopy reflectance, photosynthesis and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of the Environment*, **42**, 187–216.
- Sellers PJ, Tucker CJ, Collatz GJ *et al.* (1994) A global 1-degree-by-1 degree NDVI data set for climate studies. 2. The generation of global fields of terrestrial biophysical parameters from the NDVI. *International Journal of Remote Sensing*, **15**, 3519–3545.
- Valentini R, De Angelis P, Matteucci G, Monaco R, Dore S, Scarascia Mugnozza GE (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biology*, **2**, 199–207.
- Way JB, Rignot EJM, McDonald KC *et al.* (1994) Evaluating the type and state of Alaska taiga forests with imaging radar for use in ecosystem models. *IEEE Transactions on Geoscience and Remote Sensing*, **32**, 353–370.
- Wofsy SC, Goulden ML, Munger JW *et al.* (1993) Net exchange of CO₂ in a mid latitude forest. *Science*, **260**, 1314–1317.
- Wofsy SC, Harriss RC, Kaplan WA (1988) Carbon dioxide in the atmosphere over the Amazon basin. *Journal of Geophysical Research*, **93**, 1377–1387.