

# Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates

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## Abstract

Estimates of the seasonal absorbed fraction of photosynthetically active radiation (FPAR) and net primary productivity (NPP) are compared among four production efficiency models (PEMs) and seven terrestrial biosphere models simulating canopy development. In addition, the simulated FPARs of the models are compared to the FASIR-FPAR derived from NOAA-AVHRR satellite observations. All models reproduce observed summergreen phenology of temperate deciduous forests rather well, but perform less well for raingreen phenology of savannas. Some models estimate a much longer active canopy in savannas than indicated by satellite observations. As a result, these models estimate high negative monthly NPP during the dry season. For boreal and tropical evergreen ecosystems, several models overestimate LAI and FPAR. When the simulated canopy does respond to unfavourable periods, the seasonal NPP is largely determined by absorbed photosynthetically active radiation (APAR). When the simulated canopy does not respond to unfavourable periods, the light use efficiency (LUE) influences the seasonal NPP more. However, the relative importance of APAR and LUE can change seasonally.

*Keywords:* NPP, LAI, FPAR, seasonal, model, gradient

## Introduction

Productivity of the terrestrial biosphere depends on the ability of terrestrial vegetation to capture and use solar radiation. Although light use is influenced by other environmental factors such as climate and soil fertility, the capture of solar radiation depends solely on the structural characteristics of the vegetation. As described in Cramer *et al.* (1999), terrestrial biosphere models use different

approaches to represent vegetation structure and its variation across the globe. Differences in the representation of vegetation structure among the models may be partially responsible for the differences in annual net primary productivity (NPP) estimates among these models (Ruimy *et al.* 1999).

Kicklighter *et al.* (1999) report that differences among annual NPP estimates by these models vary across the globe as a result of differences in the magnitude and timing of monthly NPP. The largest differences occur in

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early summer in the northern boreal/temperate areas and in the dry seasons in the tropical areas. Schloss *et al.* (1999), find that the sensitivities of simulated NPP from these models to climate is modified by seasonal changes in water balance and in canopy structure, as reflected by seasonal changes in the normalized difference vegetation index (NDVI). Simulated NPP may differ seasonally, even among models that generate comparable annual estimates of NPP over large regions. The differences among models become larger as the environmental conditions become less favourable (Cramer *et al.* 1999; Schloss *et al.* 1999).

Here, we examine how differences in the representation of the vegetation canopy and its phenology influence seasonal NPP estimates. We also test the seasonality of the NPP models against seasonal satellite data using estimates of the fraction of photosynthetically active radiation (FPAR) absorbed by the canopy.

## Methods

Vegetation structure is represented, either explicitly or implicitly, in many ways among the models. Here, we focus our analysis on two of the groups described in Cramer *et al.* (1999), to highlight the importance of vegetation structure on seasonal NPP estimates: Production Efficiency Models (PEMs) and canopy models.

### *Production Efficiency Models (PEMs) (CASA, GLO-PEM, SDBM, TURC)*

Production efficiency models use NDVI data from satellites to determine FPAR. In this approach, the influences of the vegetation canopy structure and its phenology on seasonal NPP are largely represented by seasonal variations in FPAR. However, different PEMs use different algorithms to calculate FPAR from NDVI (Table 1) and different NDVI data sets. For the Potsdam NPP Model Intercomparison workshop, the FASIR-NDVI data set (Sellers *et al.* 1994) was chosen as a standard input. Although SDBM actually used the Gallo-NDVI (Gallo 1992), we include its results to examine the effect of using a different NDVI data set.

### *Canopy models (CARAIB, FBM, PLAI, SILVAN, KGBM, BIOME3, HYBRID)*

'Canopy models' simulate growth and canopy development together based on climate and other environmental factors (see 'Canopy photosynthesis models' in Ruimy *et al.* 1999). Although they represent vegetation structure differently, all models use LAI as the basis for the estimation of light absorption. For our analysis, we focus on how the models simulate phenology and estimate LAI.

To describe phenology (here we consider only leaf-on and leaf-off times), the canopy models generally use one of two different approaches (Table 2). One approach uses a separate module to estimate the timing of crucial phenological events like leaf-on/off dates without consideration of NPP. In the other approach, the phenological stages are directly determined from the current carbon balance.

To estimate LAI, models either explicitly allocate carbon to a specific reservoir to 'grow leaves', or they optimize LAI according to water or carbon balance constraints (Table 3). In the latter, the models determine the highest possible LAI that can be maintained under a given hydrological cycle, or they compute the LAI that allows the maximum NPP. In the former, the models also consider environmental constraints on LAI.

The strategies used by canopy models for describing the canopy can be summarized as follows. BIOME3 and KGBM both determine the potential LAI from available water (and carbon for BIOME3). CARAIB uses *a priori* information on the LAI of the different plant functional types (PFTs) and optimizes LAI monthly. FBM, PLAI, SILVAN and HYBRID develop LAI as a result of allocation and carbon balance. These last four models start with an LAI at or close to zero and simulate the growth of plants with increasing LAI over multiple years. Disturbances are modelled by HYBRID, resulting in fluctuations of the LAI in a pseudo-equilibrium state.

### *Methods for comparison*

As described earlier, the PEMs calculate FPAR from satellite NDVI. To compare phenology among the models, we estimate FPAR for the canopy models based on monthly LAI using the Beer-Lambert law:

**Table 1** Production Efficiency Models (PEM): Satellite-driven FPAR estimations

CASA	Linear function of the simple ratio, $SR = (1 + FASIR - NDVI) / (1 - FASIR - NDVI)$ : $FPAR = \min \{ (SR - SR_{min}) / (SR_{max} - SR_{min}), 0.95 \}$ $SR_{min} = 1.08, 4.14 \leq SR_{max} \leq 6.17$ depending on the biome (land cover map of Dorman & Sellers 1989)
GLO-PEM	FASIR-FPAR, linear function of SR: $FPAR = (SR - SR_{min}) (FPAR_{max} - FPAR_{min}) / (SR_{max} - SR_{min})$ $SR_{max}$ and $SR_{min}$ are land cover type dependent (vegetation classification of Sellers <i>et al.</i> 1994)
SDBM	Linear function of NDVI: $FPAR = -0.1914 + 2.186 \times (Gallo-NDVI)$ unlike the FASIR, there is no atmospheric correction in the Gallo-NDVI
TURC	Linear function of NDVI: $FPAR = -0.025 + 1.25 \times (FASIR-NDVI)$ calibration done employing the CESBIO-NDVI which reaches higher values than the FASIR due to additional atmospheric corrections (Ruimy <i>et al.</i> 1994)

**Table 2** Strategies used by the canopy models to simulate phenological development

	Phenological module	
	Relationship to abiotic variables	Relationship to biotic variables
CARAIB	none	all ecosystems: phenology = f(NPP)
FBM/PLAI	none	all deciduous: phenology = f(carbon balance, 'green biomass'/'structural biomass' sizes)
SILVAN	temperate deciduous: leaf-on = f(growing degree days); leaf-off = f(daily minimal temperatures)	water dependent ecosystems: phenology = f(AET/PET, NPP)
KGBM	all deciduous: leaf-on/off dates derived from satellite data time series	none
BIOME3	all deciduous: summergreen plants phenology = f(temperature) raingreen plants phenology = f(soil moisture)	none
HYBRID	cold deciduous trees: leaf-on = f(heat sums); leaf-off = f(daylength); dry deciduous trees: phenology = f(critical soil water potentials)	grass: phenology = f(NPP)

$$FPAR = 0.95 \times (1 - \exp(-k \times LAI)) \quad (1)$$

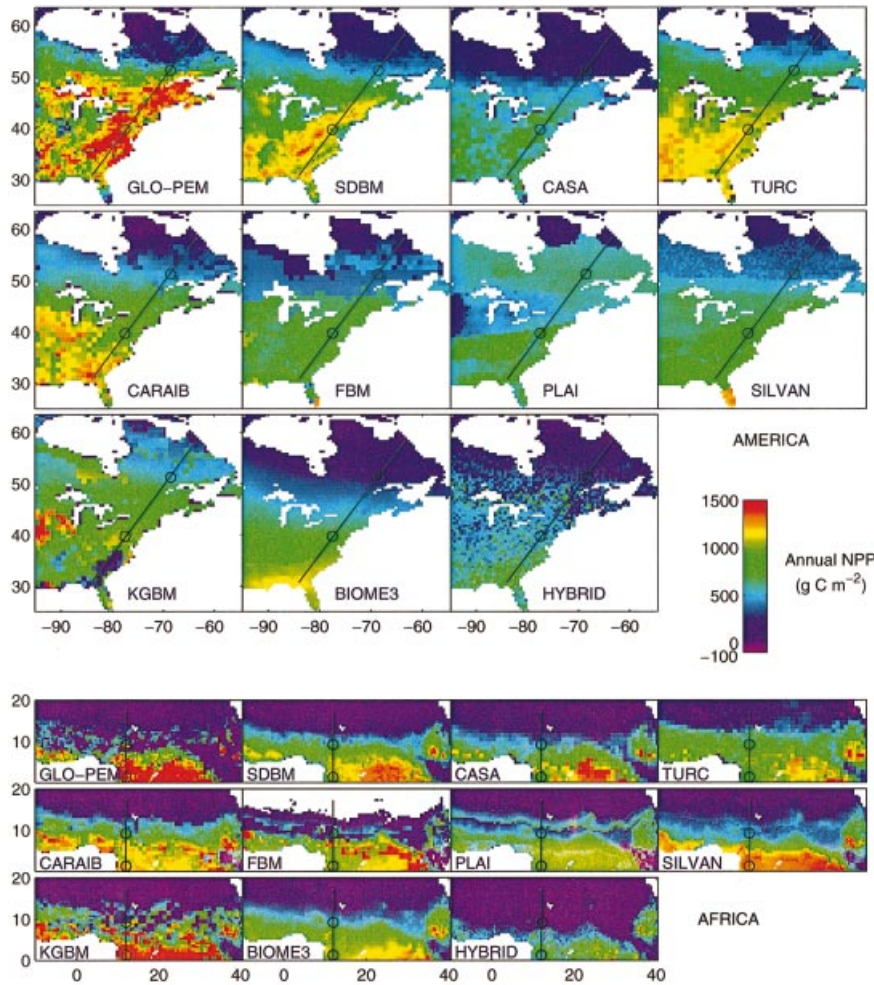
where  $k$  is the light extinction coefficient, which varies around 0.5 for green vegetation (Sellers *et al.* 1994). We use  $k = 0.5$  in this analysis, as in Ruimy *et al.* (1999).

Eqn1 is an extremely simplified formulation and does not account for the effect of the spatial heterogeneity or the clumping of the canopy (Chen 1996), but such features are largely ignored in the radiative estimates of the global NPP models anyway. However, the FPAR

value computed from Eqn1 differs from the value that would be obtained by integrating the daily interception by individual layers over depth and time, at the resolutions used by the models, because the extinction of the radiation through the canopy is nonlinear. Nevertheless, this first order computation allows the comparison of the canopy model results to the satellite derived FPAR as a diagnostic of the modelling of the radiative properties, and therefore provides a partial test of the seasonal phenological development as simulated by the

**Table 3** Strategies used by the canopy models to estimate leaf area index (LAI)

	LAI estimates	
	No explicit allocation relationship of assimilated carbon to leaves	Carbon allocation to leaves using specific leaf area (SLA)
CARAIB	minimum LAI adjusted so that annual leaf productivity is positive; maximum monthly LAI adjusted so that monthly leaf productivity is positive	none
FBM/PLAI	none	daily conversion of green biomass to leaves; green biomass/structural biomass = f (allometric relationship); carbon allocation to leaves tends to be maximized
SILVAN	none	Two steps: (1) 6-days conversion of assimilate pool to leaves; LAI/sapwood cross-sectional area = f (allometric relationship) (2) growth of leaves and sapwood until LAI maximizes NPP
KGBM	maximum yearly sustainable LAI optimized so that annual AET/PET < 1	none
BIOME3	maximum yearly sustainable LAI to optimize NPP (based on the soil moisture availability) and to satisfy the whole plant-carbon allocation requirements	none
HYBRID	none	daily allocation to leaves for grass to maximize productivity; yearly allocation to leaves for trees = f(available carbon, sapwood area, self-shading)



**Fig. 1** Maps of annual NPP over eastern North America (top) and central Africa (bottom) estimated by the 11 NPP models. The position of the transects and the location of the individual grid cells are shown. PEMs are in the first row. Calibrated canopy models are in the second row. Uncalibrated canopy models are in the third row.

canopy models. The satellite derived FASIR-FPAR dataset (see GLO-PEM in Table 1) is used as reference.

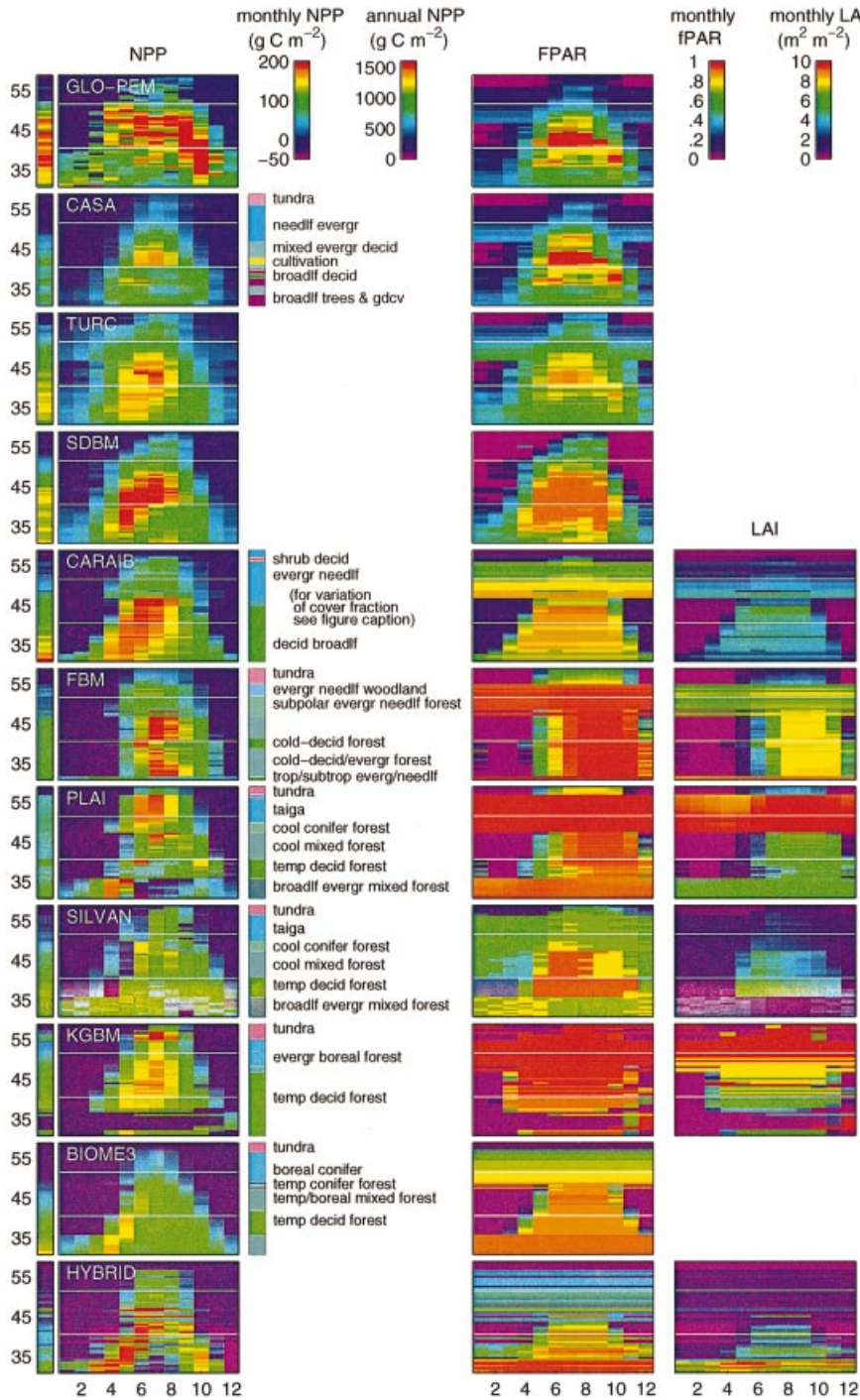
We compute Pearson correlation coefficients between the monthly FASIR-FPAR and the monthly simulated FPAR, first for the 56785 common grid cells of the

**Table 4** monthly grid cell level correlations between the modelled FPAR and the satellite FASIR-FPAR for the globe and four major ecosystems. The correlations are all significant at the 0.1% level. The first three models at the top are the PEMs, the other ones are the canopy models. GLO-PEM is not considered because the model uses the FASIR-FPAR directly

	Global	Boreal forest	Temperate deciduous forest	Savanna	Tropical evergreen forest
SDBM	0.884	0.873	0.919	0.822	0.836
CASA	0.994	0.997	0.996	0.991	0.993
TURC	0.946	0.962	0.975	0.937	0.94
CARAIB	0.736	0.683	0.613	0.711	0.301
FBM	0.6	0.351	0.728	0.498	0.173
PLAI	0.593	0.496	0.788	0.46	0.11
SILVAN	0.682	0.642	0.878	0.507	0.518
KGBM	0.563	0.420	0.742	0.559	0.154
BIOME3	0.657	0.468	0.388	0.584	0.188
HYBRID	0.696	0.351	0.728	0.498	0.173

globe<sup>1</sup>. To find out whether the relationship depends on vegetation type, we then compute the correlation coefficients for only those grid cells where the models agree on the vegetation type. We focus on: boreal evergreen forests, temperate deciduous forests, savannas, and tropical evergreen forests (3059, 3807, 4179, and 3713 grid cells, respectively). In boreal evergreen and tropical evergreen forests, many models assume that the canopy remains relatively constant during the year. In temperate deciduous forests, the canopy changes seasonally in response to changes in air temperature and solar radiation (i.e. ‘summergreen phenology’). In tropical savannas, the canopy is usually assumed to change seasonally due to changes in precipitation (i.e. ‘raingreen phenology’). As these biomes experience very different environmental conditions seasonally, the correlations between simulated FPAR and FASIR-FPAR may highlight model biases in seasonal NPP related to the representation of the canopy.

<sup>1</sup>This is more than the 41 344 grid cells in Schloss *et al.* (1999), because models such as TEM or CENTURY, which exclude wetlands, have not been analysed.



**Fig. 2** Phase diagrams of monthly NPP, FPAR and LAI (only for canopy models) along the north-south transect (radiation and temperature gradient) over eastern North America: (58.5°N, 63.5°W) to (31°N, 84°W). The horizontal axis denotes the 12 months, the vertical the latitudes. For each model, annual NPP along the transect is indicated on the left side of the phase diagram of monthly NPP, and an indication of the vegetation structure associated with each grid cell is indicated on the right side when the model uses one, either as input, or as output (BIOME3). The same colour is used to characterize similar ecosystems among different models. For CARAIB, only the forest type is indicated, but the model also uses the fraction cover of different plant functional types (PFTs) within each grid cell: forest cover fraction increases regularly from the north to the boundary between evergreen and deciduous (from 10% to 80%), while C<sub>3</sub> grass cover fraction decreases in the same direction (from 50% to 20%). Then deciduous broadleaf forests and C<sub>3</sub> plants (grasses+crops) share the southern part.

Because spatial and temporal autocorrelations may influence the above results, two transects have been chosen (Fig. 1) to analyse the seasonality of FPAR and NPP in more detail: (1) a north-south transect in eastern North America (from 58.5°N, 63.5°W to 31°N, 84°W) to examine the effects of temperature and solar radiation on seasonal NPP, LAI and FPAR in vegetation types with a summergreen phenology; and (2) a north-south transect

in central Africa (from 17.5°N, 12°E to 0°N, 12°E) to examine the effects of precipitation in vegetation types with a raingreen phenology. The first transect lies along the Appalachian mountains where the existing vegetation is close to potential, as many NPP models consider potential vegetation only (Cramer *et al.* 1999).

To examine the relative importance of canopy development and physiology on seasonal NPP estimates, we

selected two grid cells (one with evergreen and one with deciduous vegetation) from each transect and calculated monthly APAR and LUE from monthly FPAR, PAR and NPP. Monthly LUE is estimated, as in Ruimy *et al.* (1999) for annual values:

$$\text{LUE} = \text{NPP}/\text{APAR} \quad (2)$$

LUE (in g C MJ<sup>-1</sup>) is determined here as a purely diagnostic variable, synthesizing the interactions of the ecophysiological processes simulated by the models to achieve growth.

## Results

### *Evaluation of the simulated seasonal FPAR against FASIR-FPAR*

As expected, the PEMs show high correlations for the globe and the four vegetation types (Table 4) because their FPAR is derived from satellite NDVI. For CASA, which applies the FASIR algorithm with small adjustments for vegetation types, the correlations are very high. The correlations are slightly lower for TURC due to the choice of a different algorithm, and significantly lower for SDBM which uses both a different algorithm and a different NDVI data set.

For the canopy models, the relationships between simulated FPAR and the FASIR-FPAR are weaker but still highly significant (Table 4). The global correlations vary between 0.56 (KGBM) and 0.74 (CARAIB), with substantial differences among biomes. Generally, the simulated seasonal FPAR is highly correlated with the FASIR-FPAR for the temperate deciduous forests. Not surprisingly, the highest correlation occurs with SILVAN, which calibrates its phenological model for temperate deciduous forests using satellite observations. These relatively high correlations occur despite the abundance of cultivation, which affects the satellite FPAR, in land classified as potential deciduous forest. This probably reflects the fact that crops are mainly spring/summergreen, roughly in phase with temperate deciduous forests. Correlations are fairly weak for savannas, slightly weaker for the boreal forests. In these two biomes, CARAIB performs best. Correlation coefficients are generally low for tropical forests, except in SILVAN.

Overall, the canopy models represent the consequences of seasonal variations in solar radiation and temperature on canopy development in summergreen deciduous forests better than they do the seasonal precipitation on the soil water balance and canopy development in raingreen savannas.

The correlations are poorest for evergreen biomes where seasonal fluctuations of the canopy cover are limited, especially for tropical forests. Where both simulated FPAR and FASIR-FPAR indicate constant values throughout the year, a positive correlation simply indicates the agreement of the spatial variations of the FPAR values, but their absolute values may still strongly disagree. In order to better interpret these results, we now look at how seasonal NPP, FPAR and

LAI vary over the two transects. Most models simulate an increase in annual NPP southwards with corresponding increases of temperature and radiation in America or with the precipitation increase in Africa (Fig. 1). However, annual NPP estimates may vary by 2-fold among models.

### *Seasonality of FPAR, LAI and NPP along the American gradient*

*FPAR of the PEMs, FPAR/LAI of the canopy models.* The phase diagrams of seasonal FPAR along the transect (Fig. 2) reflect the results of the correlations described above for boreal and temperate deciduous forests. In general, the seasonal changes in FPAR estimated by the PEMs across the transect represent the seasonal changes in FASIR-FPAR (i.e. the FPAR for GLO-PEM) better than the FPARs of the canopy models. For the latter, the magnitude of the simulated FPAR is often much higher than the FASIR-FPAR. In both PEMs and canopy models, the FPAR associated with boreal forests and broad-leaved evergreen mixed forests in the transect varies less over the year than the FPAR associated with other vegetation types.

The seasonal patterns in FPAR are rather similar across the transect for the PEMs using the FASIR-NDVI (CASA, GLO-PEM and TURC). The highest FPAR calculated by these models occurs during the summer months around grid cells that are considered under cultivation by CASA. The overestimation of FPAR by TURC for boreal forests reflect the calibration to a different NDVI data set (Cramer *et al.* 1999) (Table 1). As expected, the seasonal pattern of FPAR estimated by SDBM varies the most from the FASIR-FPAR. Specifically, there are no sharp transitions in the seasonal patterns at the ecotones bordering boreal forests in contrast to the seasonal pattern of the other PEMs using the FASIR data. Unlike the FASIR processing (Sellers *et al.* 1994) for the boreal forest, the Gallo-NDVI used by SDBM involves no vegetation-dependent processing.

Typically, the FPAR simulated by the canopy models shows discontinuities at the ecotones. Several canopy models simulate a later FPAR increase in the spring and summer and a later decrease in autumn and winter than is indicated by the satellite-derived FPAR. The seasonal features of simulated FPAR are directly related to the seasonal estimates of LAI by the canopy models, i.e. quasi constant LAI for evergreen ecosystems and no active vegetation (LAI=0) in winter for the temperate deciduous ecosystems. The range of estimated LAI values among the models is large (e.g. from 1 to 10 for the taiga), and seems to be too high in several cases. Chen (1996) found that most boreal conifers have LAI less than 3, values may exceed 5 only in aspen/hazel stands. An LAI of 8–10 cannot be characteristic of boreal forest. There are several reasons why canopy models can simulate such high LAI values. For example, the annual LAI of KGBM is constrained by water availability only and not by carbon or nitrogen limitation. The calibration of PLAI to a high annual NPP estimate (585 g C m<sup>-2</sup> year<sup>-1</sup> following Fung *et al.* 1987) allows a very high LAI. These probably overestimated LAI generally explain the difference between the FPAR calculated from the

**Table 5** Positive correlations between the monthly NPP estimates and the monthly APAR estimates (left) or the monthly LUE estimates (right) of the different models for the four individual grid cells. Only correlations with a 0.5% significance level are indicated (NS: non significant). The first four models at the top are the PEMs, the other ones are the canopy models

Model	Boreal evergreen forest		Temperate deciduous forest		Savanna		Tropical evergreen forest	
	APAR	LUE	APAR	LUE	APAR	LUE	APAR	LUE
GLO-PEM	N.S.	0.824	N.S.	N.S.	0.945	0.779	N.S.	0.941
SDBM	1.000	N.S.	0.975	N.S.	0.972	0.940	1.000	N.S.
CASA	0.963	0.927	0.916	N.S.	0.995	0.911	0.962	N.S.
TURC	0.986	N.S.	0.992	N.S.	0.973	0.820	0.833	0.887
CARAIB	0.895	0.923	0.995	0.919	0.962	N.S.	N.S.	N.S.
FBM	0.857	0.913	0.954	N.S.	0.756	N.S.	N.S.	0.969
PLAI	0.860	0.916	0.766	N.S.	N.S.	0.992	N.S.	0.983
SILVAN	0.782	0.924	0.833	N.S.	0.985	N.S.	N.S.	N.S.
KGBM	0.792	0.965	0.972	N.S.	N.S.	N.S.	0.822	N.S.
BIOME3	0.845	0.982	0.955	N.S.	N.S.	0.995	0.980	N.S.
HYBRID	0.803	0.935	0.974	N.S.	N.S.	0.997	N.S.	0.978

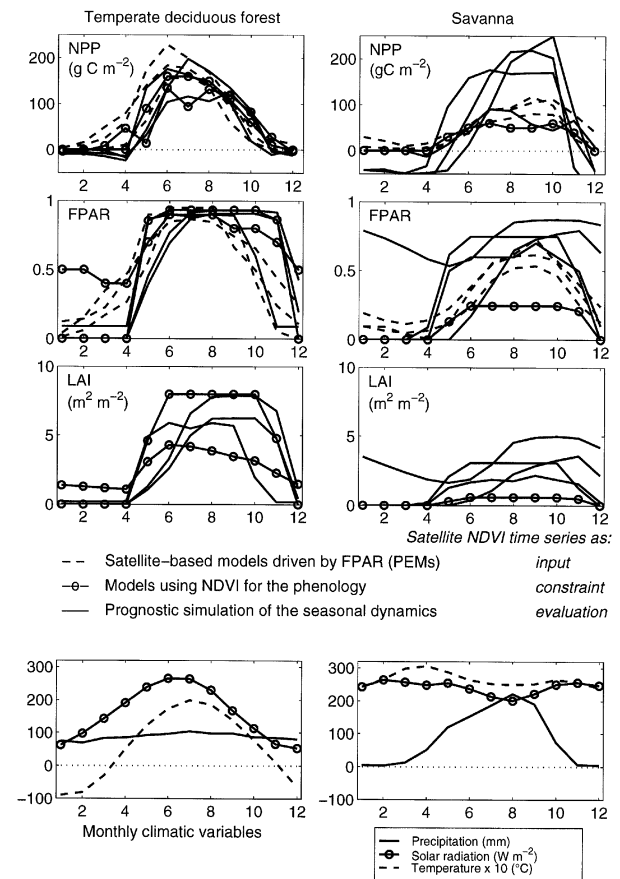
canopy models and the FPAR estimated from the PEMs in the boreal forests.

For deciduous forests, the good correlations in seasonal FPAR between the PEMs and the canopy models (Table 4) are related to: (1) similarities in simulated phenology for the canopy models and observed phenology for the PEMs, and (2) the more realistic maximum LAI (i.e. LAI ranges from 4 to 8) estimated by the canopy models. Only few LAI data exceed 6 in the temperate broadleaf deciduous forests in eastern North America (Monk *et al.* 1989). In the Harvard Forest, located near the transect, LAI in the summer is between 3 and 4 (Sakai *et al.* 1997). However, the models disagree on the timing of maximum LAI in deciduous ecosystems.

The LAI from FBM, SILVAN and PLAI tends to be spatially uniform within a biome, reflecting the importance of the calibration. In contrast, the north-to-south changes in the CARAIB-LAI of the boreal forest reflect mainly the prescribed increase of forest cover, and the high spatial variability in the HYBRID-LAI reflects the stochastic initialization of the model.

*Relationship between seasonal NPP and seasonal FPAR.* Along the American transect, the seasonality of NPP reflects, to some extent, the seasonality of FPAR (Fig. 2). For ecosystems with mainly deciduous trees, differences in the phase of seasonal NPP among models along the transect are largely determined by features of the seasonal FPAR of each model. The temporal profile of the canopy structure has a clear and profound role for determining seasonal NPP in these ecosystems. However, high monthly estimates of FPAR do not always correspond with high monthly estimates of NPP (e.g. boreal forests). Thus, other factors are also influencing the seasonal NPP estimates of these models. Similar seasonal profiles of FPAR may correspond to different seasonal profiles of NPP (e.g. CASA and GLO-PEM along the whole transect) because of different model assumptions and calibrations in the use of the absorbed solar energy (i.e.

LUE). In addition, different seasonal profiles of FPAR may relate to similar seasonal profiles of NPP (e.g. CASA and BIOME3).



**Fig. 3** monthly variations of NPP, FPAR, and LAI for two grid cells in a temperate deciduous forest (left) and savanna (right).

When monthly NPP of the boreal evergreen forest grid cell is separated into APAR and LUE, seasonal NPP is highly correlated with seasonal changes in both APAR and LUE for most models (Table 5). Although FPAR is relatively constant for boreal forests in both PEMs and the canopy models (Fig. 2), seasonal changes in solar radiation (Schloss *et al.* 1999) cause APAR to change with NPP over the year. The correlations between seasonal LUE and NPP are largely

driven by seasonal changes in temperature. Although the seasonal changes in solar radiation and air temperature are correlated (Schloss *et al.* 1999), snow and frozen soils tend to cause a time lag between solar radiation and air temperature. As a result, the seasonal changes in NPP are not completely explained by seasonal changes in APAR. Thus, estimates of seasonal NPP in boreal evergreen forests appear to be influenced mainly by seasonal changes in climate.

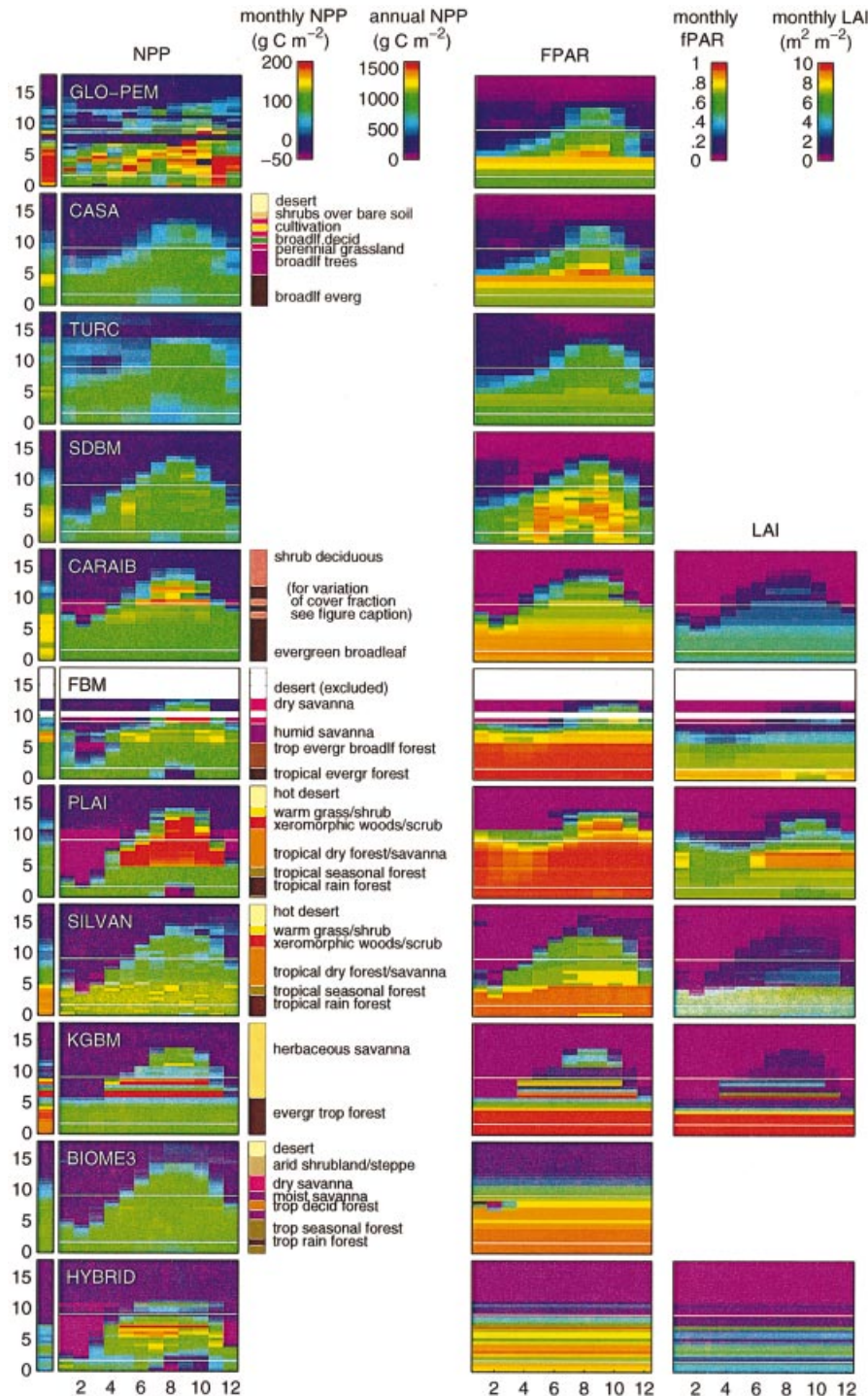


Fig. 4 The same as Fig. 2 for the north-south transect (precipitation gradient) in Africa (17.5°N, 12°E) to (0°N, 12°E). For CARAIB, the southern end of the transect has a maximum forest cover fraction (80–100%), the middle part has C<sub>3</sub> grasses and crops (around 40%), C<sub>4</sub> grasses and crops (around 20%) and forest (around 10%), and the northern part only 10% cover of C<sub>4</sub> grasses.<sup>1</sup>



In contrast, seasonal NPP in the temperate deciduous forest grid cell appears to be correlated only with APAR for most models (Table 5). For both the PEMs and the canopy models, there is generally a good correspondence between the seasonal changes in FPAR and the seasonal changes in solar radiation and air temperature (Fig. 3a). However, some of the canopy models that use a leaf-on/off strategy to describe phenology (Table 2) tend to estimate higher FPAR earlier in the year and for a longer duration than the other models. During the spring, this difference in FPAR is partly responsible for the differences in NPP, but these differences in FPAR appear to have little influence in the autumn due to low solar radiation and lower temperatures (Fig. 3a). In addition, the large variation in NPP among models during summer, when they all agree on FPAR, indicates differences in model assumptions or calibrations for the processes that drive the LUE. Thus, the relative importance of FPAR and LUE on NPP in temperate deciduous forests changes seasonally.

#### *Seasonality of FPAR, LAI and NPP along the African gradient*

*FPAR of the PEMs, FPAR/LAI of the canopy models.* Similar to the results for the American transect, the seasonal changes in FPAR estimated by the PEMs across the African transect (Fig. 4) represent the seasonal changes in FASIR-FPAR better than the corresponding FPARs of the canopy models. Again, the magnitude of the simulated FPAR of the canopy models can be much higher than the FASIR-FPAR, particularly in the southern part, but only the seasonal pattern of simulated FPAR for CARAIB, SILVAN and KGBM reflect the seasonal pattern of the FASIR-FPAR across the transect. In both the PEMs and canopy models, the FPAR for tropical evergreen forests is less variable over the year than the FPAR for other vegetation types. For the PEMs using the FASIR-NDVI, this seasonal pattern is the result of the reconstruction to a constant value through the year (Sellers *et al.* 1994). For the canopy models, the simulated FPARs again reflect the LAI estimates. Model estimates of LAI for the tropical evergreen forest grid cells of this transect vary between 3 and 12 whereas field studies have indicated that LAI can reach values of 8 or 10 for African evergreen rain forests (Walter & Breckle 1983). Although most canopy models do not estimate such high LAIs, the corresponding FPARs of these models are generally higher than the FASIR-FPAR. The low values of the FASIR-FPAR in the southern part of the transect may reflect the influence of constant cloud contamination on the NDVI signal. This raises questions about the validity of using optical satellite data to represent changes in the vegetation canopy in tropical forests. The very high estimates of KGBM presumably result from a breakdown of the limitation on LAI (cf. Table 3) in this region with little or no water limitation.

As in the American transect, the models often disagree on the distribution of vegetation used to develop NPP, LAI and FPAR estimates over the African transect. The models disagree on the northern limit of evergreen forests, with some models clearly assuming evergreen vegetation where

the satellite FPAR indicate deciduous vegetation. The models also disagree on the maximum LAI values in these regions. Some of these discrepancies result from the fact that some models consider savanna as grassland only, whereas other models simulate a mixture of trees and grasses. This could cause some models to simulate incorrect seasonality of FPAR. In the northern part, the simulated LAIs of the canopy models generally reflect the LAI observed for the Sahelian savanna at the same latitude (Hanan & Prince 1997), but some high estimates of LAI in the middle part of the transect (e.g. PLAI) are not realistic (cf. Le Roux *et al.* 1997).

*Relationship between seasonal NPP and seasonal FPAR.* The seasonality of NPP reflects, to some extent, the seasonality of FPAR over the African transect for most models (Fig. 4). However, high monthly estimates of FPAR rarely correspond with high monthly estimates of NPP. Thus, other factors are also influencing the seasonal NPP estimates. Differences in FPAR among the models may be compensated by associated differences in LUE. For example, the simulation of a green canopy in the savanna during the dry season (see Fig. 3) leads to a strong negative NPP for some models (FBM, PLAI, HYBRID) due to high respiration. As a result, the seasonal patterns of NPP from these models are similar to the seasonal patterns estimated by the other models, but with a much larger amplitude.

The correlations among NPP, APAR and LUE (Table 5) for the vegetation types in the African transect indicate that the models use different assumptions about the importance of raingreen phenology and physiology on seasonal NPP in this region. For the savanna grid cell, seasonal NPP is highly correlated with both APAR and LUE for all the PEMs. As solar radiation is relatively constant during the year (Fig. 3b), the seasonal changes in APAR reflect seasonal changes in vegetation structure (i.e. FPAR) associated with drought. The seasonal variations of the LUE due to a water stress factor (CASA, SDBM), a respiration factor (TURC), or both (GLO-PEM) also significantly influence the seasonal NPP for the savanna. In contrast, the seasonal NPP of the canopy models is significantly correlated with the seasonal changes in either APAR or LUE, but not both of these components. Seasonal NPP is influenced more by seasonal LUE in the canopy models that simulate a green canopy during drought conditions; and more by seasonal FPAR in the other models. For some calibrated models, respiration losses have to be compensated by high monthly productivity during the active period (200–250 g C m<sup>-2</sup> for PLAI and FBM and somewhat less for CARAIB). As a result, these models estimate productivity rates during the active months which are close to the efficiency of crops under optimal conditions (i.e. 1 g C MJ<sup>-1</sup> APAR). Le Roux *et al.* (1997) found a production efficiency of 0.86 g C MJ<sup>-1</sup> APAR during the growing phase and 0.58 g C MJ<sup>-1</sup> APAR at maturity in productive humid savannas.

In the grid cell covered by tropical evergreen forests, we find the least agreement among the models on the relative importance of APAR vs. LUE on estimates of seasonal NPP

(Table 5). Since the FASIR-FPAR does not change over the year, seasonal changes in APAR appear to be associated with seasonal changes in solar radiation. The seasonal changes in LUE are associated with seasonal changes in precipitation in this grid cell where relatively little rainfall occurs from June to August. CASA, SDBM, KGBM and BIOME3 indicate that seasonal NPP is influenced by APAR whereas GLO-PEM, TURC, FBM, PLAI and HYBRID indicate that LUE is more important. For FBM, PLAI, and HYBRID, the significant correlations between NPP and LUE are caused mainly by the negative monthly NPP associated with high respiration costs. For FBM and PLAI, this results from the high LAI estimates. Seasonal NPP in the grid cell covered by tropical evergreen forests is not correlated with either APAR or LUE in the CARAIB or SILVAN simulations. For these models, the soil water submodel seems to buffer the vegetation against soil moisture deficits during the dry season, so that LAI and NPP are nearly constant seasonally (see also Churkina *et al.* 1999).

## Discussion

Seasonal changes in canopy extent, as reflected in FPAR, can have a large influence on estimates of seasonal NPP. However, the relative importance of canopy extent on simulated NPP varies by vegetation type and may even change over the year within a vegetation type. The seasonal changes in the sensitivity of NPP estimates to climate variables (Schloss *et al.* 1999) are partially a result of seasonal changes in the influence of the canopy extent on simulated NPP.

The similar correlations of NPP with APAR and LUE among the models in boreal evergreen and temperate deciduous forests suggest a general consensus on the influence of the canopy extent on NPP in ecosystems with summergreen phenology. In contrast, the broad range of correlations between NPP and APAR or LUE among the models in savannas and tropical evergreen forests suggests little agreement on the influence of canopy extent on simulated NPP in ecosystems with raingreen phenology. Additional studies that collect seasonal soil moisture data concurrently with seasonal LAI and FPAR data in these ecosystems will allow a better evaluation of the relationships among these variables and improve our understanding of raingreen phenology.

### *Importance of vegetation distribution and parameterization on FPAR, LAI and NPP*

Several models treat the vegetation within each biome with a single set of parameters, including a classification as evergreen, deciduous or mixed. They generally exhibit sharp changes in the simulated variables (Figs 1, 2 and 4) at ecotones. This is also true for the PEMs that use the FASIR data, due to their processing that depends on vegetation type. Along the two transects, differences in the vegetation maps and associated parameters appear to influence the patterns of seasonal LAI, FPAR and NPP among the models

at least as much as the differences in model assumptions about ecophysiology. The spatial differences may appear as banding patterns (FBM, PLAI, SILVAN and BIOME3) or small-scale spatial variability (GLO-PEM, SDBM, CASA, TURC, CARAIB, KGBM, HYBRID) on maps of annual NPP (Fig. 1). The latter may reflect: (1) the high spatial resolution of vegetation characteristics estimated from NDVI data (SDBM, CASA, TURC, GLO-PEM, KGBM); (2) the representation of ecosystems as a mosaic of plant functional types (CARAIB) rather than a dominant vegetation type; and (3) the stochastic initialization of a dynamic component (the gap model in HYBRID).

### *Importance of calibration*

Our analysis shows that APAR and LUE may not be totally independent. When high LAI generates high APAR, costs of maintenance respiration during months with unfavourable conditions may result in low LUE. This relationship is more obvious in the calibrated canopy models than in the uncalibrated ones. It appears as if the calibrated models use parameterizations that enforce negative relationships between APAR & LUE. Ruimy *et al.* (1999) observed a negative correlation between global APAR and global LUE among the different models. They suggest that all models may (even unconsciously) be adjusted to achieve a 'commonly admitted' NPP value by being less productive if they absorb more PAR. Correctly calibrated models are required to give reasonable NPP estimates and to evaluate uncalibrated models, but the accuracy and representativeness of the field data from the ecological literature is still uneven (Kohlmaier *et al.* 1997). Field measurements of LAI may be biased toward high values that are representative of 'prime' sites chosen by ecologists rather than the average conditions in a 0.5-degree grid cell.

### *The use of satellite data for evaluating the simulated seasonal FPAR and NPP*

Field measurements of NPP usually have a temporal resolution of a few months to a year (Kicklighter *et al.* 1999). Therefore, other sources of information must be used to test the seasonal NPP estimates. In deciduous ecosystems, the positive correlations between simulated seasonal FPAR and satellite derived FASIR-FPAR provide some confidence in the models, but this does not per se constitute a validation of seasonal NPP. Models with similar seasonal FPAR can simulate very different seasonal NPP, and *vice versa*, due to different assumptions and parameterizations that determine LUE. Nevertheless, satellite data are useful for evaluating seasonal changes in vegetation structure (i.e. FPAR) that influences NPP. However, there is some variability in the phenology portrayed by the FPAR derived from different NDVI data sets and with different algorithms (cf. Figs 2, 3, and 4; and Table 4). None of the existing data sets is well enough established to be considered as a sufficiently precise evaluation tool. Furthermore, the 1-month time resolution of

the satellite data set used here is not sufficient to determine spring growth accurately and to test the simulated timing of budburst, in which a shift of 15 days may considerably change the annual estimates. NOAA-AVHRR data are affected by the orbital drift, and the information to precisely determine the effect of clouds and atmosphere is missing. Data from a generation of satellites with better quality and more appropriate bands than those from NOAA-AVHRR, along with the use of advanced algorithms to estimate FPAR (Running *et al.* 1994) should increase confidence in the use of the satellite FPAR to test the seasonality of simulated FPAR. At the same time, researchers developing canopy models may want to consider developing estimates of FPAR that are more consistent with their model assumptions to allow a more rigorous comparison of their estimates to satellite data.

## Conclusions

Seasonal changes in the canopy can have a large influence on estimates of seasonal NPP. However, the relative importance of canopy development or extent on simulated NPP varies over space and time. The canopy models do a reasonably good job of simulating the phenology of summergreen ecosystems, as indicated by satellite data. The models perform less well for the raingreen canopies, highlighting the difficulty of simulating the links between the water cycle and canopy development in these ecosystems.

Although NDVI data from satellites are useful for evaluating simulated seasonal changes in the canopy across the globe, uncertainties in estimated light use efficiencies and the calculation of FPAR prevent these data from being useful to validate seasonal NPP estimates directly.

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