

Comprehensive ecosystem model-data synthesis using multiple datasets at two temperate forest free-air CO<sub>2</sub> enrichment experiments: model performance at ambient CO<sub>2</sub> concentration

Running title: FACE model-data synthesis

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## Abstract

Free Air CO<sub>2</sub> Enrichment (FACE) experiments provide a remarkable wealth of data which can be used to evaluate and improve terrestrial ecosystem models (TEMs). In the FACE Model-Data Synthesis project (FACE-MDS), 11 TEMs were applied to two decade-long FACE experiments in temperate forests of the south eastern US—the evergreen Duke Forest and the deciduous Oak Ridge forest. In this baseline paper, we demonstrate our approach to model-data synthesis by evaluating the models' ability to reproduce observed Net Primary Productivity (NPP), transpiration and Leaf Area Index (LAI) in ambient CO<sub>2</sub> treatments.

Model outputs were compared against observations using a range of goodness-of-fit statistics. Many models simulated annual NPP and transpiration within observed uncertainty. We demonstrate however, that high goodness-of-fit values do not necessarily indicate a successful model, because simulation accuracy may be achieved through compensating biases in component variables. For example, transpiration accuracy was sometimes achieved with compensating biases in leaf area index and transpiration per unit leaf area.

Our approach to model-data synthesis therefore goes beyond goodness-of-fit to investigate the success of alternative representations of component processes. Here, we demonstrate this approach by comparing competing model hypotheses determining peak LAI. Of three alternative

hypotheses—(1) optimisation to maximise carbon export, (2) increasing specific leaf area (SLA) with canopy depth and (3) the pipe model—the pipe model produced peak LAI closest to the observations. This example illustrates how datasets from intensive field experiments such as FACE can be used to reduce model uncertainty despite compensating biases, by evaluating individual model assumptions.

Words: 249

### **Key Points**

Two temperate forest FACE experiments were simulated with 11 ecosystem models

Transpiration biases were often caused by leaf area biases

Accuracy was sometimes achieved with compensating biases in component variables

**Keywords:** model structural analysis; model benchmarking, net primary production (NPP); leaf area index (LAI); sap flow/transpiration; FACE experiment.

## 1 Introduction

The terrestrial carbon cycle is a major source of inter and intra-annual variability in the global carbon cycle [*Canadell et al.*, 2007; *Le Quere et al.*, 2009]. Many of the uncertainties in Earth System model projections are related to uncertainties in the representation of the terrestrial carbon cycle and its response to environmental change, in particular atmospheric CO<sub>2</sub> and climate [*Cramer et al.*, 2001; *Friedlingstein et al.*, 2006; *Sitch et al.*, 2008; *Forster et al.*, 2013; *Piao et al.*, 2013]. To reduce this uncertainty, there is a need to first evaluate and identify sources of uncertainty in terrestrial ecosystem and biosphere models (TEMs) and then to improve TEMs using a wide range of ecosystem data. There have been a number of studies that have evaluated TEMs against different kinds of ecosystem-scale data including eddy covariance [*Schwalm et al.*, 2010; *Dietze et al.*, 2011; *Keenan et al.*, 2012; *Schaefer et al.*, 2012] and precipitation manipulations [*Hanson et al.*, 2004; *Powell et al.*, 2013]. This paper analyses simulations from a model-experiment intercomparison project in order to evaluate model predictions against data from the ambient CO<sub>2</sub> treatments in two temperate forest Free-Air CO<sub>2</sub> Enrichment (FACE) experiments. The intercomparison involved multiple modelling groups and strong involvement from the experimentalists. This paper focuses on the ability of models to simulate ecosystems under ambient CO<sub>2</sub>, while other papers provide similar discussion for water, carbon and nitrogen cycle

responses to elevated CO<sub>2</sub>: *De Kauwe et al.*, [2013, 2014] and *Zaehle et al.*, [2014].

FACE experiments are ideal for model testing because they provide simultaneous datasets of multiple ecosystem properties at scales suitable for direct comparison with models [*Körner et al.*, 2005; *Hendrey et al.*, 1999; *Oren et al.*, 2001; *Norby et al.*, 2006; *Calfapietra et al.*, 2001; *Zak et al.*, 2011]. Situated in the south-eastern US, the two forest FACE experiments used in this intercomparison, Duke and Oak Ridge, yielded rich and detailed datasets on the state and dynamics of temperate forest ecosystems across a range of temporal scales. Some data, such as weather data and sapflow, were resolved hourly, while the length of the FACE experiments used in this synthesis (~11 years) was sufficiently long to detect relatively slow feedbacks, such as nutrient limitation [*Johnson*, 2006; *Norby et al.*, 2010]. This paper focusses on net primary productivity (NPP) and transpiration which drive carbon (C) and water fluxes—two of the main objectives of TEMs, and leaf area index (LAI) which plays a key role in simulating both NPP and transpiration by scaling leaf-level C and water fluxes to the forest canopy. Furthermore, leaf-level water C fluxes and water fluxes are linked via stomatal conductance [*De Kauwe et al.*, 2013], so that NPP, transpiration and LAI are all linked such that a bias in any one will lead to a bias in the other two. The purpose of this paper is threefold:

1. to detail the FACE model-experiment synthesis describing the two FACE experiments, the 11 TEMs and how the models were applied to the FACE sites.
2. to evaluate and compare the models and their ability to simulate key ecosystem variables that were directly measured in the FACE studies—NPP, transpiration and LAI—under ambient CO<sub>2</sub> conditions.
3. to investigate the relationship between simulated transpiration and LAI to elucidate biases in transpiration driven by biases in LAI predictions.

While this paper focuses on ambient CO<sub>2</sub> conditions, it also discusses the consequences for the prediction of responses to elevated CO<sub>2</sub> that are detailed elsewhere. Goal two above uses the FACE experimental data to assess model performance or skill in prediction of ecosystem dynamics in response to environmental variability for each of the two ecosystems (Figure 1a). Model performance is quantified using a wide range of Goodness-Of-Fit (GOF) statistics [*Nash and Sutcliffe*, 1970; *Smith and Rose*, 1995; *Moriasi et al.*, 2007], to which we apply boot-strapping to estimate confidence in the GOF metrics.

Assessing GOF does not require understanding of the underlying modelling assumptions and much can be gained from diagnosing and understanding key model assumptions that result in good fit to the data and that cause variability among model results [e.g. *De Kauwe et al.*, 2013].

Goal three above aims to synthesise model and experimental data (Figure 1b) viewing models as coherent sets of quantitative hypotheses. Key hypotheses that lead to differences in predictions across models can be identified and categorised for evaluating different modelling hypotheses and assumptions (i.e. not just the individual models) using multiple observations. The model-data synthesis approach, illustrated in Figure 1b, generates recommendations for future model development and prioritises hypotheses that require further experimental testing [Medlyn *et al.*, 2005].

Simulating the Duke and Oak Ridge FACE experiments together provides a useful comparison of the C and water fluxes in different systems (evergreen vs. deciduous) having similar climates. Simulations of annual NPP, daily transpiration and daily LAI by 11 TEMs applied to the ambient CO<sub>2</sub> treatments are evaluated as key indicators of the state and dynamics of ecosystem carbon and water cycles at the two sites. We also assess GOF of annual NPP in the context of component variables. The capacity of the model-data synthesis approach is then demonstrated by evaluating the simulation of transpiration at the two FACE experiments. We hypothesise that a component of transpiration biases are caused by LAI biases and test this using a very simple conceptual model that expresses total plant transpiration as a rate of water use per unit leaf area index (LAI), multiplied by the LAI. The method used by each model to calculate LAI is investigated, and the influence of the underlying assumptions discussed.

Finally, we consider the implications of our findings for the simulation of elevated CO<sub>2</sub> effects on ecosystem carbon and water fluxes.

## 2 Methods

### 2.1 Site descriptions

FACE experiments subject intact ecosystems to an atmosphere enriched in CO<sub>2</sub> [*Hendrey et al.*, 1999]. We simulated the Duke [*Oren et al.*, 2001; *McCarthy et al.*, 2010; *Drake et al.*, 2011] and the Oak Ridge [*Norby et al.*, 2006, p.200, 2010; *Iversen et al.*, 2011] FACE experiments located in the south-eastern USA. Both sites were situated in young (11 years old at the beginning of the experiments) closed-canopy, unmanaged plantation ecosystems. The two FACE sites were similar climatically but they differed in soil type, species composition and phenology—evergreen needleleaf dominated canopy at Duke with a deciduous broadleaf understorey and a deciduous broadleaf stand at Oak Ridge with little understorey. Initial tree and soil conditions and other site and experimental details are reported in Table 1. Experimental design, measurement protocols and ecosystem responses have been described in multiple papers, see above and below and others listed at <http://face.env.duke.edu/> and <http://face.ornl.gov/pubs.html>.

#### 2.1.1 The Duke FACE Experiment

The Duke FACE experiment [*Oren et al.*, 2001] was located within a



90ha loblolly pine (*Pinus taeda* L.-Piedmont provenance) plantation situated in the Duke Forest, Chapel Hill, North Carolina (35.97 ° N, 79.08 ° W) (Table 1). The forest is on a moderately low fertility acidic loam supporting a site index (at age 25) for loblolly pine of 16m (dominant trees were 13.2m and 11 years old at the beginning of the experiment) and rooting depths were restricted to the upper 75cm of the soil profile. The climate is typical of the warm-humid Piedmont region of the south-eastern US (mean annual temperature 15.5°C and mean annual precipitation 1150mm), with precipitation evenly distributed throughout the year. The trees were planted in 1983 at a spacing of 2m x 2.4m. Canopy closure occurred around 1998, and peak stand LAI (~6 including hardwoods) was reached in 2001 [McCarthy *et al.*, 2007].

CO<sub>2</sub> enrichment commenced in August 1996 (targeted at ambient +200ppmv) in the replicated experiment (four experimental plots in each treatment). There was heterogeneity in N availability at the site and elevated CO<sub>2</sub> experimental plots were paired (blocked) with ambient CO<sub>2</sub> control plots based on initial N availability [DeLucia *et al.*, 1999]. CO<sub>2</sub> enrichment occurred during daylight hours of the growing season targeting ambient +200ppmv. The mean elevated CO<sub>2</sub> concentration during 1996–2004 was 571 ppmv, with 92% of 1-min CO<sub>2</sub> means within 20% of the target (average target = 573 ppmv).

### 2.1.2 The Oak Ridge FACE Experiment

The Oak Ridge FACE experiment [Norby *et al.*, 2006, p.200] was located in a sweetgum (*Liquidambar styraciflua* L.) plantation on the Oak Ridge National Environmental Research Park, Tennessee (35.90 ° N, 84.33 ° W). The forest is on a low fertility silty-clay-loam supporting a site index (at age 50) for sweetgum of 23–24m (trees were 12.4m tall and 11 years old at the beginning of the experiment). The climate at the site is typical of the humid southern Appalachian region (mean annual temperature 13.9°C and mean annual precipitation 1370mm); weather records during the experiment were reported by [Riggs *et al.*, 2009]. At the start of the experiment the trees had a fully-developed canopy and were in a linear growth phase.

CO<sub>2</sub> enrichment began in May 1998 in two of five experimental plots (the remaining three plots were the control ambient CO<sub>2</sub> treatment). The FACE apparatus was constructed following the design employed at the Duke FACE experiment [Hendrey *et al.*, 1999] and CO<sub>2</sub> enrichment targeted 565ppmv. The mean elevated CO<sub>2</sub> concentration over the course of the experiment was 545ppmv, and in 1998 and 1999, 90% of 1-min CO<sub>2</sub> means were within 20% of the target [Norby *et al.*, 2001].

### 2.2 Experimental data

Over the entire course of the experiments at both sites, the most continuous and integrative data over the spatial and temporal scales of the

experiment were the measurements of NPP. NPP comprising leaf, wood and coarse root, and fine-root production was calculated from primary measurements of litter mass, specific leaf area, tree height and diameter, and minirhizotron or root ingrowth observations [Norby *et al.*, 2001, 2003; McCarthy *et al.*, 2007, 2010; Iversen *et al.* 2008; Pritchard *et al.* 2008].

Daily LAI at both sites was inferred from measurements of litterfall, specific leaf area (SLA) and canopy light interception [Norby *et al.*, 2003; McCarthy *et al.*, 2007]. At Duke, the native hardwood understorey contributed a few emergent trees to the canopy, that contributed substantially (~50% peak LAI) to the stand leaf area [McCarthy *et al.*, 2007].

Transpiration data derived from sapflow observations were available at Duke from 1998 to 2007 and for the years 1999, 2004, 2007 and 2008 at Oak Ridge. At Duke (all years), the thermal dissipation probe (TDP) technique [Granier, 1987] was used to measure sap flow in up to eight loblolly pine trees and four sweetgum trees per plot [Schäfer *et al.*, 2002; Ward *et al.*, 2013]. Duke TDP probes were vertically spaced 10 cm apart and at two depths into the sapwood (0–2 or 2–4 cm) to estimate radial sap flux. At Oak Ridge, the compensated heat-pulse technique was used in 1999 and 2004 to measure hourly sap flow at 1.3 m height and 19 mm depth for four sweetgum trees in each of two ambient and elevated CO<sub>2</sub> plots [Wullschleger and Norby, 2001]. At Oak Ridge (2007 and 2008) TDP probes were installed at

1.3 m in up to five trees in each plot [Warren *et al.*, 2011a, 2011b]. Probes were spaced vertically 5 cm apart, and installed at 1.5, 2.5 and 7.0 cm depths to estimate radial sap flux. Sap flow was scaled to total tree transpiration based on radial patterns of sap flow and sapwood depth considering potential error from a variety of sources [e.g. Ewers and Oren, 2000].

Other data collected at the sites included plant tissue N concentrations, soil water content, soil CO<sub>2</sub> efflux, soil carbon and nitrogen content and cycling, leaf physiology (photosynthesis and stomatal conductance) and tissue respiration, but these data sets were less comprehensive in their spatial or temporal coverage and were therefore less useful in this model-data synthesis.

### 2.3 The models and simulation protocol

Eleven TEMs were used in the inter-comparison: CABLE [Wang *et al.*, 2010, 2011], CLM4 [Thornton *et al.*, 2007], DAYCENT [Parton *et al.*, 2010], EALCO [Wang, 2008], ED2 [Medvigy *et al.*, 2009], GDAY [Comins and McMurtrie, 1993], ISAM [Jain and Yang, 2005], LPJ-GUESS [Smith *et al.*, 2001], O-CN [Zaehle and Friend, 2010], SDGVM [Woodward and Lomas, 2004] and TECO [Weng and Luo, 2008]. Models features are described in Table 2, and their primary functions and details are captured in a sequence of schematic images in Figure 2. Aspects of both structural similarity and diversity across the 11

models provides a good sample of ecosystem models developed over the last two decades. The models share a number of common features (Table 2), but notable differences exist that are briefly discussed in the individual model sections below.

With the exception of EALCO and ED2 (detailed in the individual model descriptions below), the simulations were initialised by spinning up the models to derive equilibrated stocks of C and N in vegetation and soils for the year 1750. Spin-ups were conducted by repeating the meteorological data recorded over the course of the experiments for 2000 years or until soil C had equilibrated. During the spin-up runs, each site was simulated assuming a deciduous broadleaf cover.

Following the spin-up, a transient 'industrial' period was simulated from 1750 to the year prior to the start of the experiment. At both sites during this period several anthropogenic disturbance events and land-use changes occurred, first clearing the 'natural' vegetation to agricultural land-use and then some fallow period before site clearance and establishment of the plantations in which the experiments occurred. This site histories (detailed in Table 1) were used to initialise the modelled forest stands at the correct age and in a transient phase of ecosystem development similar to the experimental forests. Historical CO<sub>2</sub> driving data were taken from the record used by *Vetter et al.*, [2008] created by combining the law dome ice-core record [*Etheridge et al.*, 1998] with Mauna

Loa and Antarctic flask measurements [Keeling *et al.*, 2005]. Over the multi-year course of the experiments, daytime mean CO<sub>2</sub> concentrations from the experimental observations were used. N deposition data from Dentener *et al.*, [2006] for the location of the experiments were in used in the transient phase of the spin up. During the simulations of the experiments, N deposition was fixed at a rate of 13.7 kg N ha<sup>-1</sup> yr<sup>-1</sup> at Duke [Sparks *et al.*, 2008] and 12.0 kg N ha<sup>-1</sup> yr<sup>-1</sup> at Oak Ridge [Johnson *et al.*, 2004]. Fire was not simulated as there were no fires at either site.

All models were initialised with site data to most accurately represent conditions for the Duke and Oak Ridge FACE experiments. The initialisation served to eliminate some of the parametric difference between the models and thus facilitated the model comparison. Which site data were used by each model for calibration is described in Table 3. With one exception the Duke Forest was simulated as a uniform pine plantation. ED2 was used to simulate a combined pine and hardwood forest because it has the capacity to do so and it was consistent with the normal execution of that model.

The following brief descriptions are only intended to provide the reader with the general characteristics of each of the 11 models. The reader should look to the original source material for detailed descriptions of each model.

### 2.3.1 CABLE

The Community Atmosphere Biosphere Land Exchange (CABLE) model is the Australian community land surface model designed for coupling to a number of atmospheric models and Earth System models for air pollution forecast, numerical weather and climate predictions [Wang *et al.*, 2010, 2011]. CABLE simulates energy, water, carbon (C), nitrogen (N) and phosphorus (P) cycles in terrestrial ecosystems on a sub-daily time step. CABLE was the first global model to include both N and P cycles [Zhang *et al.*, 2011] although P limitation was not enabled in the current intercomparison as neither site was considered to be P limited. Disturbance is not normally simulated by CABLE.

For this study, CABLE represented both the Duke and Oak Ridge Forests using the default evergreen needle leaf and deciduous broadleaf plant functional type (PFT) parameters [Kowalczyk *et al.*, 2007].

### 2.3.2 CLM4 (version 4.0)

The Community Land Model (CLM4) is the land surface model of the Community Earth-System Model (CESM) [Thornton *et al.*, 2007; Oleson *et al.*, 2010], simulating energy, water, C and N cycles; conserving both mass and energy. CLM4 was one of the first global C cycle models to include a mass balanced N cycle [Thornton *et al.*, 2007]. Normally CLM4 simulates fire disturbance as a function of fuel availability and soil water content

[*Oleson et al.*, 2010], though this was turned off for these simulations.

CLM4 was spun up with default PFT parameters to set initial conditions for the site (e.g., soil C), but various parameters were updated to initialize the experimental period based on site observations. N deposition was taken from the standard CLM4 dataset [*Galloway et al.*, 2004]. Also the daily fraction of mineral N lost to denitrification was changed from 0.5 to 0.1 d<sup>-1</sup> resulting in a longer residence time of mineral nitrogen within the ecosystem.

### 2.3.3 DAYCENT

DAYCENT [*Parton et al.*, 2010] is a version of the CENTURY model [*Parton et al.*, 1994] with an added vegetation component operating on a daily time-step. DAYCENT simulates C, N, and water cycles, typically for predicting soil organic C and trace gas fluxes under agricultural conditions. DAYCENT is a growth-centric model that does not explicitly simulate leaf physiology (e.g. photosynthesis, stomatal conductance). NPP is determined by a prescribed potential rate that is down-regulated by nutrient, water and temperature stress. NPP also increases, while transpiration decreases, as linear functions of atmospheric CO<sub>2</sub> concentration, the slopes of which were empirically determined using data from each site. GPP was assumed to be twice NPP and autotrophic respiration (R<sub>a</sub>) was not simulated. Disturbance is not normally simulated by DAYCENT.



#### 2.3.4 EALCO

The Ecological Assimilation of Land and Climate Observations (EALCO) model [Wang *et al.*, 2007; Wang, 2008] was developed to assimilate a wide range of Earth observation data to study the impacts of environmental change on water resources and ecosystems for applications ranging from local to continental scales. EALCO simulates energy, water, C and N cycles. A unique feature of EALCO is the dynamic coupling scheme [Wang, 2008] which uses nested numerical algorithms to solve the governing system of equations. Disturbance is not normally simulated by EALCO.

EALCO used a constrained spin-up whereby initial total soil C and N pools were prescribed with observations but the pool sizes within the total pool were spun up to equilibrium based on four years of site meteorological data. Initial plant C and N pools were prescribed with observations.

#### 2.3.5 ED2 (version 2.1)

The Ecosystem Demography (ED) model [Moorcroft *et al.*, 2001] is a complex ecosystem model which uses a forest structure approximation to scale individual-level ecophysiology, stand-level competition and landscape-level stand age distributions to regional scale dynamics. Stand structure is represented by PFT-specific, age-segregated cohorts and evolves from the competition between cohorts varying in size and stem density. ED2 uses a sub-daily time step land surface scheme to simulate

energy, water, C and N cycles within each cohort [Medvigy *et al.*, 2009]. ED2 represents fine-scale gap generation, fire, and land cover change [Albani *et al.*, 2006] and has also been used to evaluate insect disturbance, for example by the hemlock woolly adelgid [Albani *et al.*, 2010].

At both sites ED2 was run for each sample plot, initialised with the diameters at breast height (DBH) and species of each individual tree. Total soil C and N were initialized with site-level means while a short spin-up was used to initialise variables for which no measurements were available i.e. transient responses in non-structural C, litter, soil temperature and soil water content. Site data were used to adjust the southern pine and early-successional hardwood PFTs (pre-existing ED PFTs) to more closely reflect loblolly pines and sweetgum. An experimental code for dynamic fine-root allocation in response to resource limitation was also employed.

### **2.3.6 GDAY**

The Generic Decomposition and Yield (GDAY) model is a simple, daily time-step ecosystem model that represents C, N and water dynamics at the stand scale [Comins and McMurtrie, 1993; Medlyn *et al.*, 2000]. The model was originally developed as a research tool to investigate the general behaviour of CO<sub>2</sub> and N interactions [Comins and McMurtrie 1993] and therefore does not include many of the details of the other models. The

advantage of GDAY is its simplicity and tractability; the behaviour of GDAY has been analysed theoretically and is well understood [*Kirschbaum et al.*, 1994; *McMurtrie and Comins*, 1996]. GDAY was modified to represent deciduous phenology (described below) for this exercise. Disturbance is not normally simulated by GDAY.

### 2.3.7 ISAM

The Integrated Science Assessment Model (ISAM) [*Jain and Yang*, 2005] is an Earth System Model that has been used to assess responses of the terrestrial biosphere to historical changes in cropland cover, and environmental change. ISAM simulates C, N [*Yang et al.*, 2009] and water cycles. ISAM simulates secondary forest using a number of successional classes.

ISAM was applied to the two FACE sites using default PFT parameterisations and using prescribed daily LAI data at both sites.

### 2.3.8 LPJ-GUESS

The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) [*Smith et al.*, 2001] is an individual-based dynamic vegetation-ecosystem model, applicable at local to global scales. LPJ-GUESS simulates vegetation biogeography, ecosystem development, water, and C and N cycling at a daily time step. Vegetation dynamics are simulated adopting a forest gap model

approach, distinguishing different size and age classes, which compete for light and resources within a patch. The N cycle has only recently been implemented and is based on the CENTURY model [*Smith et al.*, 2013]. In standard LPJ-GUESS simulations, generic patch-destroying disturbances, representing for example windstorms, pest outbreaks or harvest, are simulated stochastically with a mean disturbance interval of 100 years. While wildfire is normally modelled prognostically based on current fuel load and soil moisture.

The planting year was calibrated, such that the simulated tree height at the beginning of the experiment corresponded with the observed tree height. The number of saplings was prescribed to match the real planting density of the dominant trees. The model was run with default PFT parameters [*Ahlstrom et al.*, 2012] using the shade intolerant evergreen needle-leaved PFT at Duke and the shade intolerant deciduous broad-leaved PFT at ORNL.

#### 2.3.9 0-CN

0-CN [*Zaehle and Friend*, 2010] a further development of the ORCHIDEE land surface model [*Krinner et al.*, 2005] that was developed to simulate terrestrial-climate feedbacks within the LMDz Earth system model [*Marti et al.*, 2005]. 0-CN simulates energy, water, C and N cycles at an hourly timescale. Disturbance is not normally simulated by 0-CN.

The model was applied in its default parameterisation, with the exception that leaf turnover time was adjusted to be consistent with the observations at Duke and the days of bud-burst and leaf senescence at the Oak Ridge sites were adjusted to match average observations.

### 2.3.10 SDGVM

The Sheffield Dynamic Global Vegetation Model (SDGVM) [Woodward and Lomas, 2004] was developed to simulate the global C cycle and global biogeography in response to climate. C and water cycles conserve mass, while canopy N is normally simulated through an empirical relationship to soil C [Woodward *et al.*, 1995]. Ecologically, SDGVM simulates a dynamic vegetation age structure and mortality occurs via self-thinning and maximum age. Fire disturbance is simulated by an empirical function of temperature and precipitation restricted by a location specific fire return interval [Kantzas *et al.*, 2013]. At these FACE sites, SDGVM was found to strongly under-predict canopy nitrogen and consequently  $V_{\text{cmax}}$ , so canopy N and the  $V_{\text{cmax}}$  to leaf N relationship was prescribed based on observed data (see supplementary material). Also, PAR was strongly over-predicted by SDGVM and so SDGVM was driven with the mean of the annual PAR cycle.

### 2.3.11 TECO

The Terrestrial ECosystem model (TECO) is an hourly time-step

ecosystem model [Weng and Luo, 2008], simulating water, C and N cycles. TECO was designed to simulate C flows in response to environmental change at specific sites [Weng and Luo, 2008, 2011]. Disturbance is not normally simulated by the TECO model.

Where data were not available default parameterisations for evergreen needle leaf and deciduous broadleaf PFTs were used with phenology parameterised to reproduce observations. The model was initialized with the initial C storage in the slow turnover pools (i.e. woody biomass and slow SOM) that it met the observed initial plant and soil C after a one year.

## 2.4 Model analysis

### 2.4.1 Goodness-of-fit statistics

We employ a number of metrics to assess and interpret model goodness-of-fit (GOF). To assess model GOF we use three metrics: model efficiency (EF), root mean square error (RMSE) and the coefficient of determination ( $r^2$ ). Most GOF metrics include the sum of squares of the predicted error (SSPE) calculated as:

$$SSPE = \sum_{i=1}^n (o_i - p_i)^2 \quad (1)$$

where  $o_i$  is the  $i^{\text{th}}$  observation,  $p_i$  is the  $i^{\text{th}}$  model prediction and  $n$  is the total number of paired observation-model comparisons. Model efficiency—EF

[*Nash and Sutcliffe, 1970*] is defined as:

$$EF = 1 - \frac{SSPE}{\sum_{i=1}^n (o_i - \bar{o})^2} \quad (2)$$

where  $\bar{o}$  is the mean of the observations across all  $n$  time steps. EF tells us how well the predictions fit the observations using the mean of the observations as a benchmark. An EF value of one represents a perfect fit and an EF above zero indicates that the simulation model predictions are a better predictor of the observed values than the mean of the observed values. The root mean square error (RMSE) is calculated as:

$$RMSE = \frac{1}{n} (SSPE)^{.5} \quad (3)$$

where  $n$  is the total number of comparisons between observed and predicted data. RMSE quantifies the mean absolute error between the predictions and observations. The coefficient of determination ( $r^2$ ) measures the proportion of variance in the observations explained by the predictions, i.e. how well the variability in the observations is captured by the predictions.

The above metrics assess GOF but they do not provide information on the sources of this error. To account for different sources of predictive error, we use Theil's inequality coefficients [*Smith and Rose, 1995*;

Paruelo et al., 1998] to decompose the variance between the observations and the modelled data, i.e. the SSPE, into three components resulting from: model bias ( $U_{bias}$ ); difference from one in the slope of observed to predicted relationship ( $U_{slope}$ ), and from random differences or non-linearity in the relationship ( $U_{error}$ ).  $U_{bias}$  describes the proportion of model error resulting from a bias (mean error Eq 6 below) and is calculated as:

$$U_{bias} = \frac{n(\bar{o} - \bar{p})^2}{SSPE} \quad (4)$$

where  $\bar{p}$  is the mean of the predictions.  $U_{slope}$  describes the proportion of model error resulting from a difference in the slope from one, most likely due to different sensitivity of the model to environmental drivers compared to observations and is calculated as:

$$U_{slope} = \frac{(\beta - 1)^2 \sum_{i=1}^n (p_i - \bar{p})^2}{SSPE} \quad (5)$$

where  $\beta$  is the slope of an ordinary least squares (OLS) linear regression of the observed on the predicted values. The observed (O) against predicted (P) regression slope was calculated using OLS linear regression with the 'lm' function in R [R Core Development Team, 2011], and this tells us whether variability in predictions is greater or less sensitive to drivers



of variability than the observations.  $U_{\text{error}}$  is the proportion of error assigned to random errors or non-linear systematic errors (such as phase changes in seasonal cycles) and is calculated as the regression residual sum of squares divided by the SSPE. To assess the magnitude of model bias we calculate the mean error (ME) between observations and predictions:

$$ME = \frac{1}{n} \sum_{i=1}^n o_i - p_i \quad (6)$$

OLS linear regressions assume that only the dependent variable is measured with any uncertainty, consequently observations should be regressed on predictions and regression of predicted values on observed values results in biased coefficients [Piñeiro *et al.*, 2008]. For this reason, we derive linear regressions of observed values to predicted values and use observed minus predicted values in equations 5, 6 and 7. Unfortunately this means that interpretation of the metrics can be non-intuitive as negative model bias means that predictions are greater than observations and vice versa. And the slope coefficient of an OLS linear regression ( $\beta$ ) describes biases in variability with a slope below one indicating that a model is more sensitive to drivers of variability than the observations, and vice versa. Most GOF statistics do not provide any assessment of statistical confidence [Moriasi *et al.*, 2007] and it is therefore difficult to assess whether GOF of one model is statistically

different from another, or even if it is statistically different from the observations. Confidence intervals for EF, RMSE and ME were calculated by bootstrapping. A distribution of values was generated by randomly re-sampling the data with replacement 1000 times and calculating a value for each resampled dataset. The 'boot' function [Canty and Ripley, 2012] in R [R Core Development Team, 2011] was used to re-sample the data and confidence intervals were based on the percentiles of the bootstrapped distributions. When referred to below, statistical significance is at  $P < 0.05$ .

#### 2.4.2 Structural analysis for interpretation of Transpiration and NPP

LAI is used to scale leaf-level calculations of water and C fluxes to the canopy in all models. LAI is simulated primarily by two processes, one that predicts the peak LAI and the other predicting the dynamics of LAI, or phenology. To analyse the model structures that determine rates of transpiration, following Schäfer *et al.*, [2002] transpiration was decomposed into two components: 1) the transpiration per unit leaf area index ( $T/LAI$ ), and 2) LAI. We further decomposed LAI into the peak LAI ( $LAI_{peak}$ ) and the phenological state as a proportion of  $LAI_{peak}$  ( $LAI_{phen}$ ):

$$T = T/LAI \cdot LAI = T/LAI \cdot LAI_{phen} \cdot LAI_{peak} \quad (7)$$

The decomposition allows model transpiration to be corrected for biases in model LAI by replacing either, or both, modelled  $\text{LAI}_{\text{phen}}$  and  $\text{LAI}_{\text{peak}}$  by observed values. This simple decomposition assumes that transpiration is proportional to LAI, which is an over-simplification that breaks down when the difference between modelled and observed LAI are large. Nevertheless, this approach is useful for attributing differences among models in transpiration to differences in the LAI components. Examining differences in the assumptions that lead to modelled  $\text{LAI}_{\text{peak}}$  and  $\text{LAI}_{\text{phen}}$  then allows us to identify some of the reasons for different predictions among the models.

Following *Zaehle et al.*, [2014] we also use the simple decomposition of NPP into component variables, N uptake ( $N_{\text{up}}$ ) and N use efficiency (NUE). NUE is defined as  $\text{NUE} = \text{NPP}/N_{\text{up}}$ , such that  $\text{NPP} = N_{\text{up}} \times \text{NUE}$ . The decomposition separates the N constraint on NPP into the stoichiometric constraint (NUE, the N required for growth), and the N uptake constraint (the N available for growth).

#### **2.4.2.1 Modelling peak LAI**

Peak LAI depends on leaf growth, leaf turnover (litterfall) rate and specific leaf area (SLA). Often turnover plays a lesser role in determining peak LAI than leaf allocation and growth due to differential timing of these two processes. For some models LAI is the primary variable and leaf allocation is adjusted to maintain or achieve a target LAI. The models in

this synthesis use either fixed partitioning coefficients, allometric scaling or an optimisation approach to simulating LAI or leaf growth.

Using fixed partitioning coefficients, 'fractions of the assimilated carbon [are] allocated to each organ' [*Franklin et al.*, 2012]. Leaf growth is simulated by multiplying total C available for growth (i.e. NPP) by a foliage partitioning-coefficient. CABLE, CLM4 and GDAY used fixed coefficients. SLA was a prescribed model parameter with the exception of CLM4 where SLA increases linearly with canopy depth leading to an exponential increase in LAI with leaf C. Both GDAY and CLM were parameterised with observed leaf partitioning coefficients. CABLE applied PFT default, fixed coefficients that varied according to phenological phase.

Allometric scaling is when 'relationships between organs [...] vary with individual size but not with the environment' [*Franklin et al.*, 2012]. ED2, LPJ-GUESS and O-CN all use allometric scaling, maintaining a prescribed constant LAI:sapwood area ratio at maximal foliar development, according to the pipe-model hypothesis [*Shinozaki et al.*, 1964]. The pipe-model implies a functional relationship whereby sapwood area must be sufficient to supply the canopy water demand resulting from a given LAI. The mass of wood needed to maintain a given sapwood area increases with tree height, therefore the leaf mass:wood mass ratio decreases with tree height. Therefore peak LAI is constrained by increasing wood growth demands

as trees increase in size. Using the pipe-model, peak LAI is also sensitive to the rate of sapwood turnover to heartwood. ED2 simulates LAI as a function of DBH within each cohort, scaling to the stand scale by stem density and cohort land area. LPJ-GUESS parameterised LAI:sapwood area ratios with observations while O-CN used PFT defaults. These models typically also assume a functional balance between leaf and root mass, such that the requirement for uptake of water and nutrients, which scales with root mass, increases with leaf mass and resource limitation.

SDGVM optimises peak LAI based on the principle that over one year the sum of leaf C and annually integrated respiration of the lowest LAI layer should not exceed annually integrated C assimilation of that layer. DAYCENT, EALCO and ISAM constrained peak LAI using observed values. Thus the hypotheses used to simulate LAI include: fixed partitioning coefficients of NPP based on general PFT relationships (CABLE); fixed partitioning coefficients with a linear decrease in SLA through the canopy (CLM4); the pipe-model (ED2, LPJ-GUESS and O-CN) and an optimisation to maximise canopy C export (SDGVM).

#### **2.4.2.2 Modelling LAI phenology**

Phenology is determined by the interaction of bud burst, leaf growth rate and leaf turnover rate. Bud-burst (or initiation of needle growth) was simulated using either an empirical calibration of phenology with climatic

data or passively, i.e. no specific model structure controlling timing and the dynamics of leaf biomass are an emergent property of leaf growth and litterfall. For evergreen PFTs, CLM4 and GDAY simulated phenology passively while LPJ-GUESS assumed no seasonal variation in LAI. For evergreen PFTs, ED2 and O-CN only simulated active timing of litterfall, rapid needle growth occurs in the spring when C assimilation increases and when the LAI:sapwood area ratio is below the target.

In contrast to simulation of evergreen PFTs, deciduous leaf C dynamics in CLM4 and GDAY were entirely controlled by phenology; all C for leaf growth comes from C stored in the previous year and the timing leaf growth and litterfall were entirely determined by active phenology routines. CABLE, CLM4, GDAY, LPJ-GUESS and SDGVM represented bud-burst and senescence in seasonally deciduous PFTs (and for evergreens in CABLE and SDGVM) using algorithms calibrated with satellite derived phenology and climate observations (variously cumulative growing degree days-GDD, day length and soil temperature) [White *et al.*, 1997; Botta *et al.*, 2000; Smith *et al.*, 2001; Zhang *et al.*, 2004; Picard *et al.*, 2005]. DAYCENT, EALCO, O-CN and TECO calibrated a formulation of bud-burst with site observations based on either: running mean air temperature, GDD or GDD and soil temperature, respectively. For this study ED prescribed deciduous phenology but is more generally based on GDD. ISAM used daily LAI as a model input (repeating 2007 in 2008). TECO initiates leaf growth with stored C, then

leaf C allocation is a fixed fraction of C allocated to growth, which is a function of available C and temperature, until maximum LAI is reached. TECO simulates maximum LAI as a function of tree height, therefore peak LAI is either the achieved maximum or is an emergent property of the dynamics of leaf growth and turnover.

### 3 Results

#### 3.1 Simulation of annual NPP and transpiration at ambient CO<sub>2</sub>

Model predictions of annual NPP and transpiration under ambient CO<sub>2</sub> are compared against measurements in Figure 3a-d and many models were within the bounds of observational uncertainty. Clear outliers were CLM4 and SDGVM, which strongly over-predicted NPP at both sites; ED2 which over-predicted NPP at Duke and under-predicted NPP at Oak Ridge; and ISAM which under-predicted NPP at Duke. A majority of models captured either the magnitude or the inter-annual variability in observed annual NPP, and EALCO and LPJ-GUESS captured both (Figure 3a,b). There was no evidence to suggest that NPP was better captured by models which better represent light interception and canopy scaling by numerically solving C assimilation in each of a number of canopy layers (EALCO, ED2, LPJ-GUESS, SDGVM & TECO-Figure 2).

Several models (EALCO, ED2, GDAY, O-CN, SDGVM and TECO) captured the decline in NPP at Oak Ridge from 2003/4 to 2007 (Figure 3b) but most of these models (with the exception of O-CN and GDAY) also showed an increase

in NPP from 2007 to 2008, which was not consistent with the data. Models that show a general NPP decline but an increase in 2008 (ED2, SDGVM and TECO) may have not simulating the strength of N limitation by the end of the experiment at Oak Ridge [Norby *et al.*, 2010] or may also have missed carry-over effects from the strong drought in 2007 [Warren *et al.*, 2011b].

For annual transpiration at Duke (Figure 3c), most models were within the observed range of uncertainty though there was a general over-prediction in the later years of the experiment. SDGVM consistently over-predicted annual transpiration while GDAY, ISAM and TECO consistently under-predicted annual transpiration (Figure 3c). At Oak Ridge, the mean model prediction of annual transpiration was generally low-biased when compared against the four years of data (Figure 3d). However, the mean results from a wide range of model results.

Goodness-of-fit (GOF) statistics of model predictions with data are shown in Figure 4 (Duke) and 5 (Oak Ridge). For annual NPP, the model efficiency (EF) 95% confidence intervals (95% CIs) for most models contained zero (Figures 4a and 5a), indicating that those models were no statistically better or worse than the mean (across years) of the observations as predictors of annual NPP. That is, the models captured the mean annual NPP or some of the inter-annual variability but not both—to be better than the mean of the observations as a predictor of those observations might be considered a minimum standard for model performance.



However the EF confidence intervals were wide, indicating that for a given model there were large year-to-year differences in prediction accuracy. RMSE and ME CIs were also wide, however statistical differences between the models and observations were more apparent in these measures of error. Therefore, overall model errors in annual NPP were detectable, but 11 years of data were insufficient to accurately assess model ability to capture inter-annual variability in NPP using EF. Higher frequency transpiration data were available so discussion of transpiration GOF is deferred to daily transpiration in the section below.

A notable exception from large EF uncertainty in annual NPP was EALCO at Oak Ridge which had a highly significant, high EF (Figure 5a). The spin-up method for EALCO resulted in high initial soil organic matter in rapidly cycling pools which declined over time and decreased N availability, resulting in declining NPP. The declining trend of NPP in EALCO was overlain by accurate reproduction of inter-annual variability; however, EALCO did not submit results for 2008 which separated models with a decreasing NPP trend into those driven by climate and those by declining N availability.

Many of the models RMSE 95% CIs were overlapping with or just outside of the 95% CI of the annual NPP observations (Figure 4b and 5b). The strong biases of CLM4, ED2 and SDGVM were reflected by significantly negative EF (Figure 4a and 5a) and large RMSE (Figure 4b and 5b). Theil's coefficients

(Figure 4f and 5f) show these errors to result from large mean error (ME) biases ( $\pm 300 \text{ gC m}^{-2}\text{y}^{-1}$ —Figure 4d and 5d). At Duke, ISAM, GDAY, O-CN and TECO also had MEs (Figure 4d,f) which led to poor prediction of annual NPP, reflected in high RMSEs (Figure 4b). Despite negative EF scores, CLM4 and SDGVM captured a significant amount of inter-annual variability at Duke (and Oak Ridge for SDGVM), reflected in the significant ( $P < 0.05$ )  $r^2$  values (Figure 5c and 6c).

NPP results from many integrated processes and can be viewed as something of a composite variable that integrates multiple processes. It is possible that compensating biases exist whereby biases of opposite sign in component processes can offset each other when combined into the composite variable which results in spuriously high GOF. Different conclusions of model skill can be drawn by analysing some of the component processes of NPP compared to NPP alone. Figure 6 shows the decomposition of NPP into two component variables—N uptake ( $N_{\text{up}}$ ) and N use efficiency (NUE)—[Zaehle *et al.*, 2014] in the ambient treatment at both sites. Two of the three models that best captured NPP at Oak Ridge (EALCO and O-CN) over-predicted  $N_{\text{up}}$  and under-predicted NUE resulting in good predictions of NPP. In other words, the models that correctly simulated the magnitude of observed NPP, were doing so with compensating biases in component variables. CABLE at Duke and GDAY at Oak Ridge most accurately captured all three variables NPP,  $N_{\text{up}}$  and NUE. C and N dynamics are the focus of another study within the FACE-MDS

[Zaehle *et al.*, 2014].

All of these models represent N uptake and NUE in different ways. NUE is determined by tissue C:N stoichiometry and the partitioning of new growth between various tissues with different C:N stoichiometry. Various assumptions are made on the flexibility of tissue stoichiometry, varying from fixed, to flexible within prescribed bounds, to flexible [Zaehle *et al.*, 2014]. Partitioning assumptions are also diverse, as touched upon above and discussed in detail in *De Kauwe et al.*, [2014]. A caveat for comparisons to observations of NUE and N uptake are that the measurements are not independent and depend upon scaling assumptions and sampling uncertainty. Nevertheless, the variability in the predictions of NUE show that the modelling assumptions that determine NUE are crucial in predicting NPP.

### 3.2 Simulation of daily transpiration and LAI at ambient CO<sub>2</sub>

#### 3.2.1 Duke Forest

At Duke, there were significant modelled errors in both the magnitude and timing of daily transpiration (Figures 4, 5 & 7, Table 4). Many models (CABLE, CLM4, EALCO, LPJ-GUESS, O-CN, and SDGVM) overestimated transpiration over the year or during the peak season, while TECO consistently underestimated transpiration through the year and ISAM underestimated transpiration in the spring (Table 4).

The comparisons with LAI data at Duke Forest were confounded by the broadleaf component of the forest (predominantly in the understorey) that significantly contributed to the whole stand LAI (Figure 3e and see *McCarthy et al.*, [2007]). Models represented the mixture of evergreens and broadleaves in multiple ways as a result of different representations of forest structural heterogeneity, and only ED2 represents vertical structure of different PFTs within the forest stand. The variability across models in representation of the PFT heterogeneity at Duke invariably confounds the comparison to observations, therefore the discussion of transpiration in relation to LAI at Duke is deliberately limited as comparing the representations of forest structure is beyond the scope of this analysis. Interestingly ED2, which resolved vertical stand structure and individual tree distribution, over-predicted peak LAI despite detailed parameterisation of stand structure, DBH and LAI:DBH. The LAI over-prediction was caused by higher than observed NPP (Figure 3a and 4d) which led to over-prediction of DBH growth and thus through the DBH:LAI relationship, LAI.

In some models (CLM4, O-CN, and SDGVM) the high summer transpiration biases at Duke (Figure 7a) were matched by high summer biases in stand LAI (Figure 3e). The remaining models with high summer transpiration bias (CABLE, EALCO and LPJ-GUESS) also had high LAI biases when compared to the pine LAI only (Figure 3e); suggesting that perhaps the pines, which

comprised most of the canopy leaf area (i.e. not including the understorey), were the primary contributors to stand transpiration. None of the models (ED2, GDAY, ISAM and TECO; Table 4) with low biased daily transpiration showed a low LAI bias. By contrast, all models that showed high biases in transpiration in spring, summer and autumn (CABLE, CLM4, DAYCENT, LPJ-GUESS, O-CN, and SDGVM) also exhibited high biases in LAI.

**3.2.2 Oak Ridge Forest** Many models at Oak Ridge under-predicted daily transpiration over the whole season or during the peak season (see CABLE, DAYCENT, ED2, GDAY, ISAM and TECO) in Figure 7b). TECO had a low, mid-season LAI bias but in contrast with transpiration biases, LAI biases were a result of non-systematic error caused by a general low bias, a shifted peak LAI followed by a late season high bias. For DAYCENT the low mid-season transpiration bias was not matched by a low mid-season LAI bias (Figure 3f). With both positive and negative transpiration biases (Figure 7b), DAYCENT transpiration errors were a result of non-systematic error (Figure 51), while LAI biases were strongly affected by a large ME caused by very late onset of senescence (Figure 3f). In contrast to transpiration biases, LAI simulations by ISAM and ED2 had a slope bias below one and a negative ME.

CLM4 was the only model to simulate a high transpiration bias over the whole season at Oak Ridge (Table 4, Figure 7b) and CLM4 showed the

strongest LAI bias of all models (Figure 3f). CLM4 maintained a significant LAI bias in the mid-season (Figure 3f and 5p&r) while transpiration biases were reduced (Figure 7b), CLM4 also had higher transpiration errors during the early season and showed early initiation of bud-burst. CABLE simulations of transpiration and LAI were high biased throughout the winter season (Table 4). CABLE, CLM4, DAYCENT, GDAY, LPJ-GUESS, O-CN and SDGVM showed significant early and late-season errors in transpiration at Oak Ridge (Figure 7b). Theil's coefficients show that non-systematic error was a major source of error between predictions and observations of daily transpiration in the deciduous Oak Ridge forest (Figure 5l). Non-systematic error includes both random error and error caused by phase or period shifts in the seasonal cycles which changes the sign of the error over the course of the year. LPJ-GUESS and SDGVM showed a clear phase shift in predicted daily transpiration demonstrated by the opposing sign of the errors in the spring and autumn, LAI predictions of these two models were also out of phase with the observations (Figure 3f). O-CN showed a smaller phase shift with errors most pronounced in the early season as were the LAI errors (Figure 3f). EALCO showed some small transpiration errors in the early and late season that were also apparent in LAI predictions.

DAYCENT showed positive transpiration errors in the early and late seasons, i.e. an increase in transpiration period, and the LAI seasonal cycle was also of increased period. However, transpiration errors were

larger in the spring while LAI error was more pronounced in the autumn. Transpiration errors in GDAY were negative in both the spring and autumn (Figure 7b) while LAI was only smaller than observed in the spring (Figure 3f). ED2 showed some early season high bias in LAI that was not matched by transpiration errors.

### 3.2.3 Correction of transpiration error for LAI error

We used a simple conceptual model (Eq 7) as an aid to detect and quantify transpiration errors caused by biases in phenology and biases in peak LAI. The simple model assumes that the relationship of transpiration to LAI is linear, which is a simplification but one that is useful and has been used previously [e.g. Schäfer *et al.*, 2002]. Because the dual (conifer plus hardwood) stand structure at Duke was not represented by the majority of models we only apply the correction of transpiration for LAI biases (as described by Eq 7) at Oak Ridge (Figure 8). Reductions in RMSE represent improvements in the simulation of daily transpiration once corrected for the components of the LAI bias, while increases in the RMSE mean that correction for LAI biases make transpiration errors worse indicating compensating errors between simulating the biophysics of transpiration (transpiration per unit leaf area) and LAI.

At Oak Ridge, CABLE, DAYCENT, ED2, ISAM and TECO showed negative mid-season errors in transpiration. CABLE and TECO also simulated a low peak

LAI, which when corrected for slightly improved simulations of transpiration (Figure 8). Although correction for peak LAI in CABLE reduced mid-season transpiration errors it also increased the winter errors, therefore there was an interaction when correcting for both peak LAI and phenology that improved transpiration simulation by 22%. In contrast, TECO transpiration errors were extremely negative (Figure 7b) and while correction of peak LAI improved simulation of transpiration over the year, correction for phenology made simulations worse. So when corrections were combined there was little change in TECO transpiration error indicating an extremely low bias in simulating the biophysics of transpiration in TECO.

Correction for the small peak and phenology LAI biases in ED2, GDAY and ISAM increased the transpiration RMSE by ~28-40% (albeit against a lower baseline RMSE, Figure 5h). Although the errors in the mean seasonal LAI cycle were small (Figure 3f) there was inter-annual variability in both phenology and peak that caused LAI errors (for ISAM which prescribed LAI this was because 2007 LAI was used repeated in 2008). The increase in transpiration RMSE when corrected for LAI suggests that LAI biases in ED2, GDAY and ISAM were compensating biases in the simulation of the biophysics of transpiration.

CLM4 transpiration errors were improved once corrected for LAI phenology bias and peak LAI bias individually. However, correction for both LAI biases simultaneously did not further improve the RMSE (Figure 9),



suggesting that the phenology bias (when LAI errors were largest) caused transpiration errors but that the overall high LAI bias was compensating a low bias in the simulation of transpiration per unit leaf area.

For some models with an early-season transpiration bias (CABLE, LPJ-GUESS, and SDGVM), correction of transpiration for the LAI phenology bias improved the simulation of transpiration by up to ~40% (Figure 8). LPJ-GUESS and SDGVM both showed a late-season low transpiration bias and LAI bias. In LPJ-GUESS, senescence was too rapid while senescence in SDGVM was initiated too early (Figure 3f). The correction of transpiration for LAI biases (modelled  $T/LAI$  multiplied by observed LAI) only works if modelled transpiration is non-zero, which was not the case in the late season for these models. Therefore accurate simulation of LAI phenology in both LPJ-GUESS and SDGVM would likely improve transpiration simulation even more than suggested by the reduction in RMSE once corrected for LAI phenology bias.

Transpiration errors of DAYCENT and O-CN were not improved when corrected for phenology bias, despite positive errors in both transpiration and LAI during the spring. Both models also had negative transpiration errors during the late season (day 250–300) but positive LAI errors over the same period, therefore early season transpiration errors were reduced by LAI phenology correction in the early season, but were increased during the late season. There was little change in EALCO transpiration RMSE when

corrected for LAI because both phenology and peak LAI were prescribed.

#### 4 Discussion

Many of the models reproduced annual NPP, and daily transpiration, in ambient CO<sub>2</sub> conditions with a reasonable degree of accuracy. However we have shown that for some models, accuracy in prediction of both annual NPP and daily transpiration was achieved by biases of opposing sign in component variables—NUE and N uptake for NPP and transpiration per unit LAI and LAI for transpiration—what we call compensating biases in component processes. If we had drawn conclusions of model performance based only on the GOF statistics in Figures 4 and 5, we would have missed the compensating biases and could have had false confidence in many of the models. Without analysing N uptake and NUE, EALCO would have been considered the most accurate predictor of NPP, however, Figure 6 shows that overall GDAY was a more accurate predictor of NPP and its component variables under ambient CO<sub>2</sub> conditions. For a full analysis of the compensating biases in the C and N component processes of NPP in response to elevated CO<sub>2</sub> see *Zaehle et al.*, [2014].

The underlying principle of multi-model benchmarking is to find the 'best' or most predictively accurate models given experimental data as a benchmark. Many variables are composites of other variables, for example NPP is the product of nitrogen use efficiency and nitrogen uptake [*Zaehle*

*et al.*, 2014], or biases in  $V_{\text{cmax}}$  parameterisations can be compensating biases in the representation of photosynthesis and canopy scaling [*Bonan et al.*, 2011]. Therefore it is possible, and we have shown, that accurate GOF for one variable can result from compensating biases among component variables, variables which one may not be able to test for GOF due to unavailable data. We advise caution in interpretation of GOF metrics where potential compensating biases are impossible to assess or could be overlooked, as this could lead to false confidence in model performance.

Based on the EF statistic, as predictors of annual NPP most of the models were statistically indistinguishable from the mean of the observations. However, uncertainty in NPP EF for most models was large indicating that 11 years of annual data were insufficient to accurately assess model ability (GOF) at simulating inter-annual variability. In part the uncertainty in evaluating model performance at simulating annual NPP was due to variable model sensitivities to drought convolved with the impact of and subsequent recovery from stochastic events; such as an ice-storm at Duke [*McCarthy et al.*, 2006b] and a severe wind event at Oak Ridge [*Warren et al.*, 2011b]. Stochastic events and subsequent recovery were not simulated by the models. There was some evidence to suggest that models captured observed reductions in NPP in response to drought (see 2002 at Duke and 2007 at Oak Ridge; Figure 3a&b), although there was a broad range of responses in these years across the models. Sensitivity of the models to

drought results from variable representations of soil water dynamics, the form of the physiological response function, and whether C assimilation, stomatal conductance or both are affected. Modelled C and water fluxes are sensitive to the soil water stress assumptions [e.g. *De Kauwe et al.*, 2013; *Powell et al.*, 2013] and model-data synthesis could help to progress our understanding of how to accurately represent soil water stress. Without assessing the uncertainty in EF, had the models been ranked according to EF we would have missed the conclusion that the uncertainty was too large to really distinguish one model from another. To avoid false confidence in models' abilities to predict an ecosystem function it is critical to fully understand the competing models' structures and the hypotheses which they represent. Often understanding deviations of complex model results from those of a simple, tractable model can help to identify important component processes as demonstrated by the simple relationship proposed between transpiration and LAI [for another example see *De Kauwe et al.*, 2013]. Once competing hypotheses have been identified appropriate analyses can be developed to compare competing hypotheses to the data [for an example see *Zaehle et al.*, 2014; *Rastetter et al.*, 1992].

Further reducing the generality of interpretations of GOF accuracy to broader regional or global scales is that models were initialised using site specific data, including disturbance/land-use history, soil characteristics and plant traits. We do not have these data for every model

grid square at larger spatial scales, abstracting most of the models from their normal mode of operation in which representative PFT traits and natural successional processes are assumed.

In this study, LAI, in particular phenology, was best simulated by models that used some form of calibration to site data, which in turn facilitated accuracy in the simulation of transpiration (Table 4 and Figures 3&7). However, it is not desirable nor possible to use site data to calibrate regional or global model simulations and the applicability of global trait relationships [e.g. *Kattge et al.*, 2009] or simulating adaptive traits [e.g. *Pavlick et al.*, 2013; *Scheiter et al.*, 2013] could also be tested. Global databases of land-use history are becoming available and land-use change in global C cycle simulations has been shown reduce the 20th Century land C sink [*Gerber et al.*, 2013]. While beyond the scope of this current set of simulations, a sensitivity analysis of the models used in this inter-comparison to various components of site history would make a useful study.

#### **4.1 The relationship of LAI and transpiration**

We have shown that biases in LAI—both in the peak and phenology—result in biases in the simulation of transpiration. For example, SDGVM simulates early onset of leaf growth and senescence (Figure 3) and this leads to similar seasonal transpiration biases (Figure 7). As another

example, CABLE does not explicitly represent stored C in plants; rather, the LAI over the winter months for deciduous forests represents stored C for spring leaf growth. This formulation predictably leads to transpiration biases over the winter months in deciduous PFTs.

LAI is a key ecosystem property and model variable that scales leaf gas-exchange to the canopy, determines light capture (absorbed photosynthetically active radiation-APAR) and the biophysical inter-action with the atmosphere [Richardson *et al.*, 2010, 2013]. Correction of LAI biases will lead to improved simulation of transpiration (Figure 8) which in models (e.g. CABLE) coupled to atmospheric circulation models will improve the representation of the biophysical feedback of the land surface on the climate system. However, we have also demonstrated that some models had compensating biases in the simulation of transpiration, these compensating biases must be resolved before improvement LAI simulation accuracy will result in improved transpiration accuracy. In the following sections we examine the model hypotheses that determine peak LAI and LAI phenology and assess these competing hypotheses based on the experimental observations. Many models calibrated either peak LAI or LAI phenology to observations. As calibration is not a predictive method we do not discuss these models in detail in the relevant sections below.

#### 4.1.1 Peak LAI

For modelling peak LAI, the biological theories represented by the

models are, fixed partitioning coefficients and SLA (CABLE, DAYCENT, GDAY), the pipe-model (O-CN, LPJ-GUESS and to an extent ED2), optimisation for canopy C export (SDGVM) and fixed partitioning combined with a linear increase in SLA through the canopy (CLM4). Both CLM4 and SDGVM over-predicted LAI, while O-CN and LPJ-GUESS made a reasonable approximation.

CABLE, DAYCENT and GDAY all use the partitioning coefficient approach (see above). The ability of these models to reproduce peak LAI depended on accurate simulation of NPP and whether they used site data to parameterise SLA and leaf partitioning coefficients. At Oak Ridge, GDAY simulated peak LAI close to the observations (Figure 3f) using partitioning coefficients and SLA parameterised with the site data. As turnover at the site was minimal prior to peak LAI (and did not occur until peak LAI was reached in GDAY), accurate simulation of NPP resulted in the accurate simulation of peak LAI. CABLE was a poorer predictor of peak LAI at Oak Ridge because generic plant functional type (PFT) parameters were employed.

CLM4 also uses the partitioning coefficient approach, but strongly over-predicted LAI due to the assumption of a linear increase in SLA through the canopy [Thornton and Zimmermann, 2007]. A linear increase in SLA means that each additional LAI layer is less costly in terms of leaf C than the previous layer. Thus as NPP increases, leaf C increases at the same rate but LAI increases at an exponential rate (Supplementary information 1). CLM4 was parameterised with site data for SLA at the top of

the canopy, the rate of increase of SLA through the canopy, and leaf C partitioning. However, the over-prediction of NPP led to an even greater over-prediction of peak LAI.

The default mode of CLM4 increases wood partitioning as a function of NPP, and all other parameters necessary to simulate allocation and LAI are fixed so that LAI can be written as a function of NPP (Supplementary information 1). The relationship between LAI and NPP for broad classes of CLM4 PFTs is shown in Figure 9, demonstrating that over-prediction of LAI is likely to be a common feature of CLM4 especially for broadleaf deciduous PFTs.

While increasing SLA with canopy depth is a valid assumption [*Norby and Iversen, 2006; White and Scott, 2006; Lloyd et al., 2010*], the formulation of CLM4 leads to over-prediction of LAI within the range of forest NPP (Figure 9). Constraining SLA to a maximum value [*White and Scott, 2006*] would limit the over-prediction of LAI. The pipe-model imposes area:volume scaling between leaf area and sapwood volume which would also constrain LAI at high productivity, though this would require representation of tree structure in CLM4.

SDGVM strongly over-predicts peak LAI. LAI in SDGVM maximises canopy C export by targeting an annual C balance (assimilation - respiration - leaf C construction costs) of zero in the lowest LAI layer. The optimisation is sensitive to model parameterisation of canopy N scaling and



dark respiration, which may have been misrepresented. Also the optimisation does not account for the structural C necessary to support the lowest LAI layer (as posited by the pipe-model), nor supporting root tissue [McMurtrie and Dewar, 2013], which could be missing costs from the optimisation calculation that could help to constrain LAI.

O-CN and LPJ-GUESS employ the pipe-model to simulate allocation, of which peak LAI is an emergent property, and both models accurately reproduced peak LAI at Oak Ridge. Using the pipe-model, LAI is sensitive to the LAI:sapwood area ratio, sapwood turnover and SLA. Other than SLA, both O-CN and LPJ-GUESS used default PFT parameters. The reasonable reproduction of Oak Ridge LAI by both models suggests that with accurate simulations of NPP, the pipe-model assumption is relatively robust, constraining LAI within the bounds of the observations (Figure 3f). It is well established that there is a relationship between leaf area and sapwood area as proposed by the pipe-model [Shinozaki *et al.*, 1964; Oohata and Shinozaki, 1979] although the exact nature of the relationship is still the subject of some debate [McDowell *et al.*, 2002; Schneider *et al.*, 2011].

#### 4.1.2 LAI phenology

CLM4, ED2 and GDAY all simulate phenology passively (as described in the methods) for evergreen PFTs. In GDAY passive phenology resulted in no seasonal cycle in pine LAI at Duke (Figure 3e), and restricted amplitude of

the cycle for CLM4 and ED compared with observations. The restricted amplitude of CLM4, ED2 and GDAY resulted from a constant needle turnover rate, in contrast to the observations, which showed distinct seasonality with a senescent phase during the late season (Figure 3e and see *McCarthy et al.*, [2007]). LPJ-GUESS assumes no variability in evergreen LAI over the year, in clear contrast to the observations. The remaining models used similar methods to simulate phenology at both sites so we discuss them in combination.

In contrast to the observations at Oak Ridge, CABLE simulates a canopy with an LAI between 1-2 during the winter months as a reserve to initiate physiological activity in the following spring. Predictably the over-prediction of winter LAI led to over-prediction of winter transpiration (Figure 7 and 8). Prioritised partitioning of NPP in TECO at Oak Ridge caused the timing of peak LAI in TECO to be delayed until immediately before senescence. Timing of the peak LAI was delayed because the initial, rapid leaf growth phase was not sufficiently long to achieve the peak LAI. The delay was exacerbated by the default SLA in TECO being ~20% lower than observations, slowing the accumulation of LAI.

At Oak Ridge the sweetgum were of a more northerly provenance and hence had delayed bud-burst compared to local trees, somewhat confounding the evaluation of the timing of leaf growth. However, LPJ-GUESS (at Oak Ridge) and SDGVM (at both sites) initiated bud-burst extremely early in the

year (Figure 3e,f). The SDGVM phenology formulation uses a cumulative growing degree day (GDD) formulation that was evaluated in Siberia [*Picard et al.*, 2005], which may not be more generally applicable to temperate regions. GDAY and CLM4 accurately reproduced the timing of bud-burst at Oak Ridge using the formulation of *White et al.*, [1997], most likely because the formulation was calibrated using North American data. CABLE also reproduced bud-burst accurately using the satellite formulation of *Zhang et al.*, [2004].

CABLE, CLM4 and GDAY all accurately reproduced the timing of leaf growth initiation and senescence, however there were notable differences in rates of leaf growth and senescence which lead to marked differences in their ability to reproduce the seasonality of LAI at Oak Ridge (Figure 3). The only difference between GDAY and CLM4 was the parameterisation of the duration of the leaf growth and senescence season but had important consequences for reproducing the timing of transpiration. Timing of senescence in SDGVM occurs when leaves reach a fixed age and therefore early senescence was tied to early bud-burst.

At Oak Ridge most models prescribed or calibrated LAI phenology (DAYCENT, EALCO, O-CN and TECO) in some way with observations. And if not calibrated at the site scale to empirical data, phenology schemes were calibrated at the regional or global scale. While several of the regional calibrations of satellite observations of greenness to climate data [*White*

*et al.*, 1997; *Zhang et al.*, 2004] captured phenology at the two sites reasonably, such calibrations are limited in their mechanistic representation of leaf growth initiation in spring. And a large suit of models have been shown to perform poorly at a wider range of sites in North America [*Richardson et al.*, 2012]. A primary reason for deciduous phenology is the avoidance of frost damage to leaves [*Woodward*, 1987] and a growing degree day (GDD) formulation of bud-burst assumes that the risk of frost is simply a function of GDDs. However this assumption may not be valid in the warm humid climate of the south-eastern US, and perhaps multiple environmental indicators may be employed to predict frost risk, and hence bud-burst, more accurately.

#### 4.2 Potential consequences for simulating responses to elevated CO<sub>2</sub>

LAI biases have been shown to be important in modelled GPP biases [*Richardson et al.*, 2012; *Schaefer et al.*, 2012] and LAI biases are also likely to affect the magnitude and seasonality of the GPP response to elevated CO<sub>2</sub> (eCO<sub>2</sub>). Low LAI ecosystems have more opportunity to increase the fraction of absorbed photosynthetic radiation (*f*APAR) as *f*APAR saturates as LAI increases. FACE experiments have shown that the peak LAI response [*Norby and Zak*, 2011] and the response of *f*APAR [*Norby et al.*, 2005] to elevated CO<sub>2</sub> are higher in low LAI systems. Low LAI systems are also likely to have a greater response to eCO<sub>2</sub> [*Ewert*, 2004] as a higher

fraction of the canopy is light-saturated. Light-saturated photosynthesis is more sensitive to  $e\text{CO}_2$  because at light saturation  $e\text{CO}_2$  relieves substrate limitation of the Calvin-Benson cycle which increases the carboxylation rate of RuBisCO [Farquhar *et al.*, 1980]. However, at Duke NPP responses to  $\text{CO}_2$  were strongly related to LAI responses [McCarthy *et al.*, 2006a] and more generally, NPP response to  $e\text{CO}_2$  in low LAI systems was often directly proportional to the response of  $f\text{APAR}$  [Norby *et al.*, 2005], suggesting that the NPP response in low LAI systems could be mostly explained by the increase in LAI.

Despite reasonable predictions of the magnitude of NPP by many models (Figure 3a,b) they achieved such projections with considerable inaccuracies in their underlying N cycle simulations (Figure 6c,d). For example, almost every model strongly over-predicted N uptake at Oak Ridge, including the model with the best reproduction of NPP (EALCO). Similar results were observed for transpiration. Correcting transpiration in GDAY, ED2 and ISAM for LAI resulted in worse simulation of transpiration which suggests that the LAI bias was compensating a transpiration bias of opposite sign.

The problems that the models have simulating ecosystem state and dynamics at ambient  $\text{CO}_2$  are likely to affect their performance at simulating ecosystem response to elevated  $\text{CO}_2$ . N cycling interacts with C cycling and plays a major role in the response to elevated  $\text{CO}_2$  of the Duke and Oak Ridge forests [McCarthy *et al.*, 2010; Norby *et al.*, 2010; Drake *et*

*al.*, 2011; *Garten et al.*, 2011] and the models used in this study to simulate these ecosystems [*Zaehle et al.*, 2014]. For example, the lower than observed NUE simulated by many of the models (Figure 4c,d) results in the simulated forest using and sequestering more N which may exacerbate the strength of the simulated N limitation under elevated CO<sub>2</sub> [*Zaehle et al.*, 2014].

Similarly model biases at simulating transpiration are likely to bias ecosystem responses to elevated CO<sub>2</sub> via the effect of CO<sub>2</sub> decreasing stomatal conductance. Decreased stomatal conductance is likely to increase soil water content which is likely to impact transpiration and primary productivity [*Schäfer et al.*, 2002; *McCarthy et al.*, 2010; *Morgan et al.*, 2011; *De Kauwe et al.*, 2013]. In summary, model development is still necessary to reduce model uncertainty in simulating ecosystem C, N and water dynamics in ambient CO<sub>2</sub> conditions to provide an accurate baseline from which to make confident predictions of terrestrial ecosystem dynamics on a rising CO<sub>2</sub> Earth.

#### 4.3 Concluding remarks

Models are tools that can be used used to interpret terrestrial ecosystem dynamics in response to observed or manipulated environmental change. They are also requisite tools for making projections associated with future environmental change. As a measure of the quality of these

tools we assess their ability to predict some key aspects of current terrestrial ecosystems or the biosphere—e.g. carbon fluxes and water fluxes. We have shown that model accuracy in key ecosystem properties is sometimes achieved with compensating biases which are likely to bias model predictions of ecosystem dynamics in response to environmental change. Compensating biases demonstrate that we cannot use GOF statistics alone as metrics for the predictive ability of a model. The use of GOF statistics without consideration of compensating biases could result in over-confidence in a model's predictive ability which could ultimately result in misguided environmental policy.

To provide a more useful approach to interpretation of model results we advocate the comparison of models, to each other and with experimental data, based on their underlying hypotheses and assumptions (Figure 1). The model-data synthesis method draws multi-model inter-comparisons into the scientific method of hypothesis, prediction and experiment. Finally we encourage a more iterative process of model inter-comparison and experimental data synthesis to help identify, and therefore facilitate reductions in, uncertainty in model predictions to further our understanding of the biosphere.

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Table 1. Site characteristics

	Duke FACE	Oak Ridge FACE
Location	Orange County, North Carolina 35° 58' N, 79° 06' W Elevation 163 m	Roane County, Tennessee 35° 54' N, 84° 20' W Elevation 230 m
Soil Classification (US)	Ultic Hapludalf	Aquic Hapludult
Soil texture	acidic loam (49% sand, 42% silt, 9% clay)	silty-clay-loam (21% sand, 55% silt, 24% clay)
Soil C content (Mg ha <sup>-1</sup> )	101	74
Soil N content (Mg ha <sup>-1</sup> )	3	8
Mean annual Temp (° C)	15.5	13.9
Mean annual precipitation (mm)	1145	1371
N deposition (kg ha <sup>-1</sup> y <sup>-1</sup> )	13.7	12–15
Site history (used in model initialisation)	Pre-1800, deciduous broadleaf forest. 1800, clear cut to grassland 1920, forest establishment allowed . 1982, clear-cut and burned, and plantation established.	Pre-1750, deciduous broadleaf forest. 1750, clear cut to C4 crop. 1943, grassland established. 1988, plantation established.
Dominant species	<i>Pinus taeda</i> (L)	<i>Liquidambar styraciflua</i> (L)
Main other species present (understory unless specified)	<i>Liquidambar styraciflua</i> (some canopy trees), <i>Ulmus alata</i> , <i>Acer rubrum</i> , <i>Cornus florida</i> .	<i>Elaeagnus umbellata</i> , <i>Microstegium vimineum</i> , <i>Lonicera japonica</i> , <i>Acer negundo</i> , <i>Liriodendron tulipifera</i> , <i>Lindera benzoin</i> .

Nominal elevated CO <sub>2</sub> concentration (ppm)	Ambient +200	565
Treatment duration	1994–2010	1998–2009
Age at initiation	11	11
Number of plots	4 elevated, 4 ambient (1994 – 1996 1 plot per treatment)	2 elevated, 3 ambient
Plot size (m <sup>2</sup> )	527	314
Number trees per plot	86 <i>P. taeda</i> and 140 canopy and subcanopy broadleaved individuals > 2cm at 1.3 m	~90 <i>L. styraciflua</i>
Initial dominant height (m)	13.2	12.4
Initial peak Leaf Area Index (LAI)	3.8	5.5
Initial basal area (m <sup>2</sup> ha <sup>-1</sup> )	32.5	29
Initial stem + branch mass (kg C m <sup>-2</sup> )	4.0	3.6
Initial leaf mass (kg C m <sup>-2</sup> )	0.3	0.17
Initial coarse root mass (kg C m <sup>-2</sup> )	0.9	1.4
Initial peak fine root mass (kg C m <sup>-2</sup> )	0.1	0.37
Initial leaf C:N	— <sup>a</sup>	24.3
Initial wood C:N	—	365
Root C:N <sup>b</sup>	—	67

<sup>a</sup> no data

<sup>b</sup> ambient treatment mean

Table 2. Operational, structural and physiological characteristics for the eleven models that simulated the FACE experiments.

Model	CABLE	CLM4	DAY- CENT	EALCO	ED2	GDAY	ISAM	LPJ- GUESS	O-CN	SDGVM	TECO
Version	2.0	4.0	---	---	2.1	---	---	---	---	070607	---
Modeller(s)	Wang, Y- P.	Thornton	Parton	Wang, S.	Dietze	De Kauwe Medlyn	Jain	Wärland Hickler	Zaehle	Walker	Weng Luo
Model structure and concept											
Initial Conditions	Spun up	Spun up	Spun up	Specified & Partial spin up	Specified & Partial spin up	Spun up	Spun up	Spun up	Spun up	Spun up	Spun up
Dynamic Vegetation	No	No	No	No	Age structure	No	No	Age structure	None	Age structure	None
N mass balance	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes
Leaf N	Pred.	Obs.	Pred.	Pred.	Obs	Pred.	Obs	Pred.	Pred.	Obs	Pred.
Roots	Distribut ed	Distribut ed	Distribut ed	Distribut ed	Distribut ed	No	No	Distribut ed	Distribut ed	Distribut ed	Distribut ed

Carbon (and N) pools		Accepted Article									
Biomass pools <sup>a</sup>	L, W, R	S	CR, FR	FR	WH, R, S	R	LG, RG	HW, FR	F, S	HW, CR, S	L, W, FR
	L, SW, HW, CR (L & D) FR, L, B, W, CR, L, WS, L, B, SH, HW, L, W, R, L, WS, L, W, FR, L, SW,										
	Pipe- model, resource capture, phased phenology fractions										
C Partitioning	Fixed fractions	Fixed fractions									
	, phased phenology	Fixed fractions	Phased phenology	Fixed fractions	Pipe- model & resource capture	Fixed fractions	Fixed fractions	Pipe- model & resource capture	Pipe- model & resource capture	Optimal leaf & fixed fractions	Fixed fractions
	phenology fractions										
Litter soil C pools	3	4	2	3	1	4	4	2	6	4	1
SOM soil C pools	3	4	3	3	3	3	4	3	4	4	By layer
Physiological Characteristics <sup>b</sup>											
empirical											
Photosynthesis	Farquhar N, SW	Collatz N, SW	GPP = 2*NPP	Farquhar leaf $\Psi$	Farquhar N	Farquhar N, SW	Farquhar	Collatz N	Kiang N, SW	Farquhar N, SW	Farquhar N
Canopy layers	1	1	1	10	10+	1	1	10+	10	LAI	10+
Sun & shade leaves											
Yes	Yes	Yes	No	Yes	No	No	Yes	No	Yes	Yes	Yes





Table 3. List of site-specific parameters and data used to calibrate the individual models.

model	site	Parameters Prescribed but variable with time	leaf traits	physiological traits	stoichiometry	C partitioning	soil properties
CABLE	Duke	-	-	-	-	-	-
CLM4	-	-	Top-of-canopy SLA, leaf lifespan	-	leaf C:N, wood C:N, leaf litter C:N	Fine root growth to leaf growth ratio, stem growth to leaf growth ratio	texture
DAYCENT	-	-	SLA	$A_{\max}$ (including $\text{CO}_2$ response), transpiration response to $\text{CO}_2$	-	-	texture, water holding capacity, bulk density
EALCO	-	-	SLA, max LAI	$V_{\text{cmax}}/J_{\text{max}}$ to N relationship	-	Target C ratios among foliage, sapwood and fine root biomass	texture
ED2	-	-	SLA	$V_{\text{cmax}}$	leaf C:N, wood C:N	leaf and stem allometry	texture
GDAY	-	-	Leaf lifespan (assumed the same for roots)	$V_{\text{cmax}}/J_{\text{max}}$ to N relationship	-	NPP partitioning to leaves, wood & fine roots.	water holding capacity
ISAM	LAI (daily)	-	-	-	-	-	-
LPJ-GUESS	-	-	SLA	-	-	-	texture, water holding capacity
O-CN	-	-	SLA	-	-	-	texture, water holding capacity
SDGVM	Canopy N (annual)	-	SLA	$V_{\text{cmax}}/J_{\text{max}}$ to N relationship	-	-	texture, water holding capacity, bulk density
TECO	-	-	SLA	-	-	-	water holding capacity



Table 4. Seasonal biases in transpiration and LAI at Duke and Oak Ridge.

Biases were judged based on the GOF statistics presented in Figures 4 and 5, and the comparisons to data in Figures 3e&f and 7a&b. + refers to a high bias, • no bias, and - a low bias. A combination of symbols indicates that the model exhibited a combination of those biases in that season.

model	variable	Duke spring	summer	autumn	winter	Oak Ridge spring	summer	autumn	winter
CABLE	Transpiration	•/+	+	+	•	+/-	-	-/+	+
CLM4		+	+	•	•	+	+	+	•
DAYCENT		•/+	•	•	•	+/-	-	-/+	•
EALCO		•/+	+	+	•	+	•	•/+	•
ED2		•/-	•	•	•	•/-	-	-	•
GDAY		•	-	•	•	•	-	-/•	•
ISAM		-	•	-	•	•/-	-	-/•	•
LPJ-									
GUESS		+	+	•/+	•	+	•	•/-	•
O-CN		•/+	+	•	•	•/+	•	•	•
SDGVM		+	+	•/+	•	+	•	-	•/+
TECO		-	-	-	•	•/-	-	-	•
CABLE	LAI	•	+	+	•/+	+/-	-	-/+	+
CLM4		+	+	+	+	•/+	+	+	•
DAYCENT		+	+	+	+	•/+	•	+	+/•
EALCO		•/+	+	•/+	•	•	•/+	+	•
ED2		+	+	+	+	•	•/+	•	•
GDAY		+	•	+	+	-	-/•	•	•
ISAM		•/-	•/-	•	•	•	•	•	•
LPJ-									
GUESS		+	+	+	+	+	•	•/-	•
O-CN		+	+	+	+	•/+	•	+/-	•
SDGVM		+	+	+	+	+	•	-	•/+
TECO		+	+	+	+	•/-	-	-/+	•

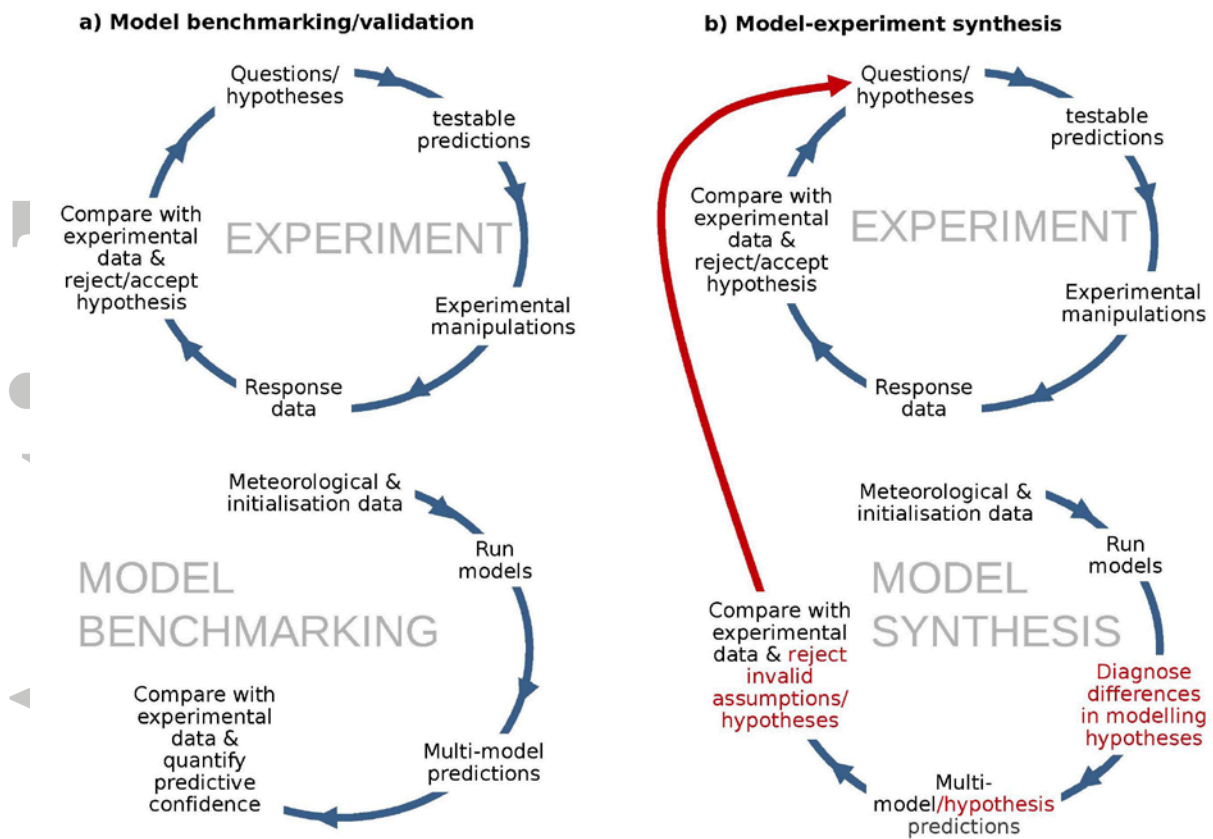


Figure 1. A schematic diagram of model-experiment data interactions a) assessment of Goodness-Of-Fit (GOF) of model predictions to experimental data (benchmarking), and; b) model-experiment synthesis. The differences of model-experiment synthesis and benchmarking are highlighted in red. For model-experiment synthesis the modelling loop feeds back into the experimental loop, and another arrow could even be drawn whereby predictions are initially generated by the collection of hypotheses represented by a suite of models which feed directly into the experimental cycle.

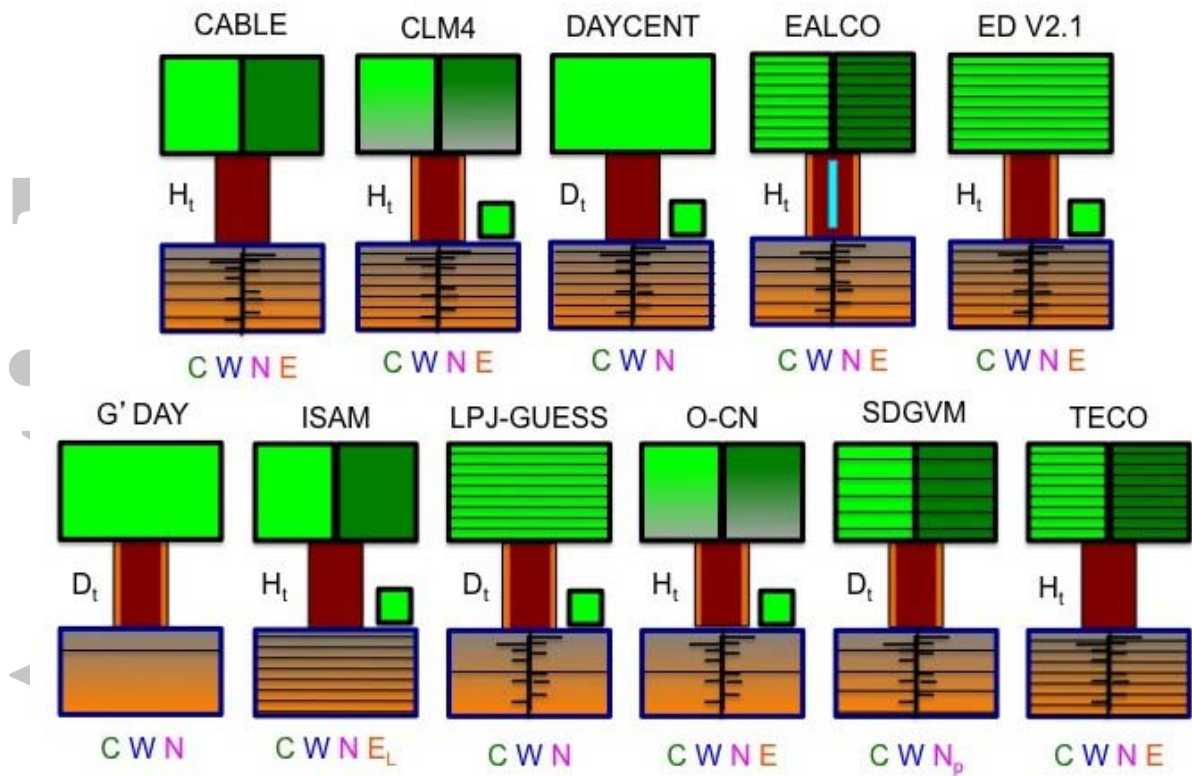


Figure 2. Structural representations of the eleven models used in the FACE model inter-comparison. Canopy layering and sun/shade assumptions are designated for each model. A single versus dual coloured stem section indicates independent sapwood and heartwood simulations. Those models with a sub-canopy 'green box' include a ground-level vegetation component. Belowground details indicate soil layering and the presence or absence of roots. A Belowground horizontal lines represent the approximate level of layering for that model. D<sub>t</sub> and H<sub>t</sub> indicate daily and hourly time steps, respectively. Letters subtending each model diagram indicate the presence of carbon (C), water (W), and nitrogen (N where N<sub>p</sub> is partial) cycles and the execution of a full energy balance (E where E<sub>L</sub> is leaf only). EALCO includes stem water capacitance. Additional model details are itemized in Table 2.

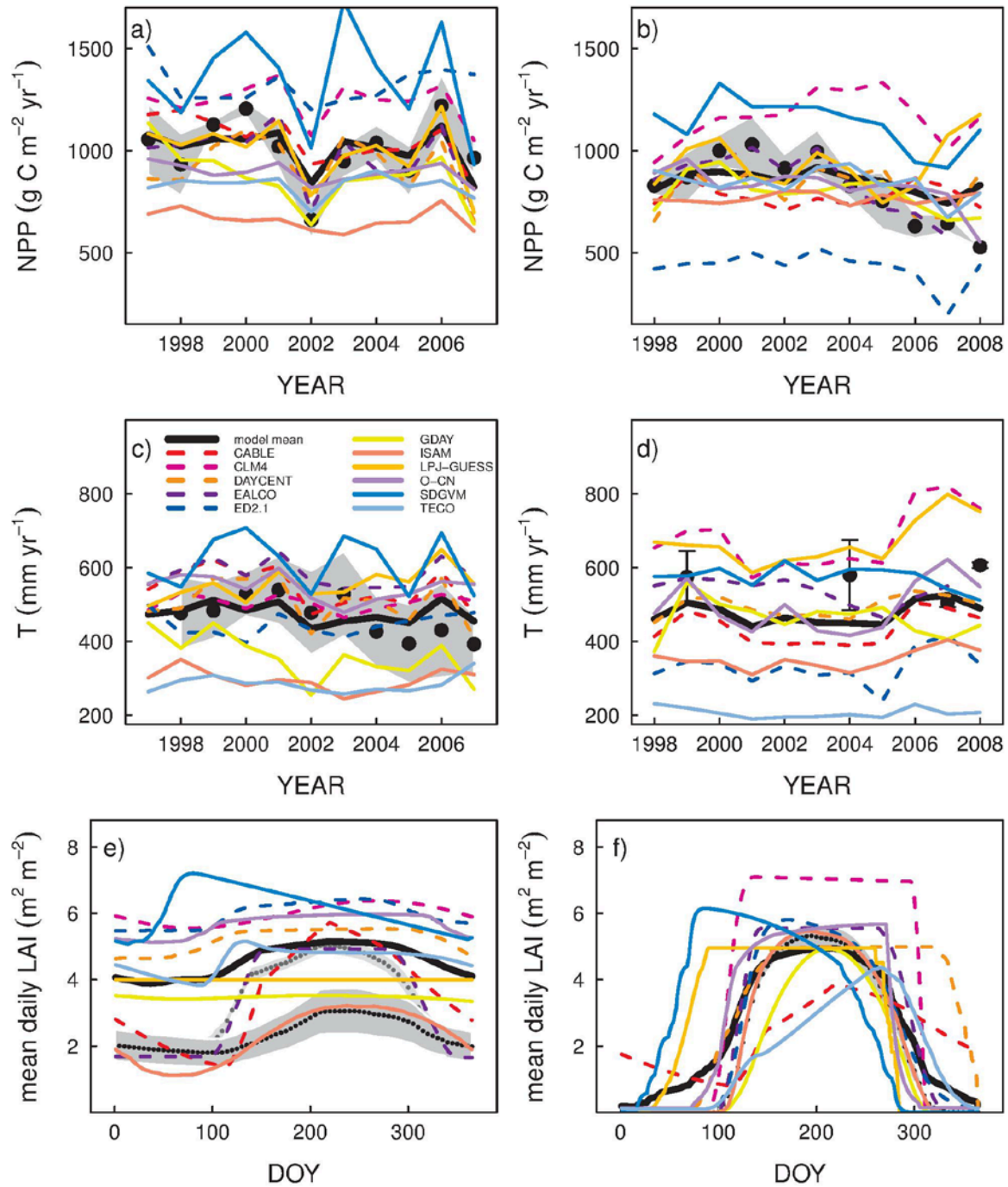


Figure 3. Annual net primary production (NPP; g C m<sup>-2</sup>y<sup>-1</sup>; a,b), annual transpiration (mm y<sup>-1</sup>; c,d) and daily mean LAI (m<sup>2</sup>m<sup>-2</sup>; e,f) at Duke (a,c,e) and Oak Ridge (b,d,f) for the ambient treatments. The mean of all model results is represented by the thick black line. Model results are represented by the coloured lines, observed results by the black circles with the 95% confidence interval (CI) shaded in grey. Where data are present for limited years the 95% CI's are shown by error bars (see plot d), where no error bars are visible they are within the space occupied by the data point. Observations on plot e show both the pine LAI (lighter grey shading and grey circles) and the whole stand LAI (i.e. including broadleaved LAI). For clarity, LAI points are shown only every 5 days.



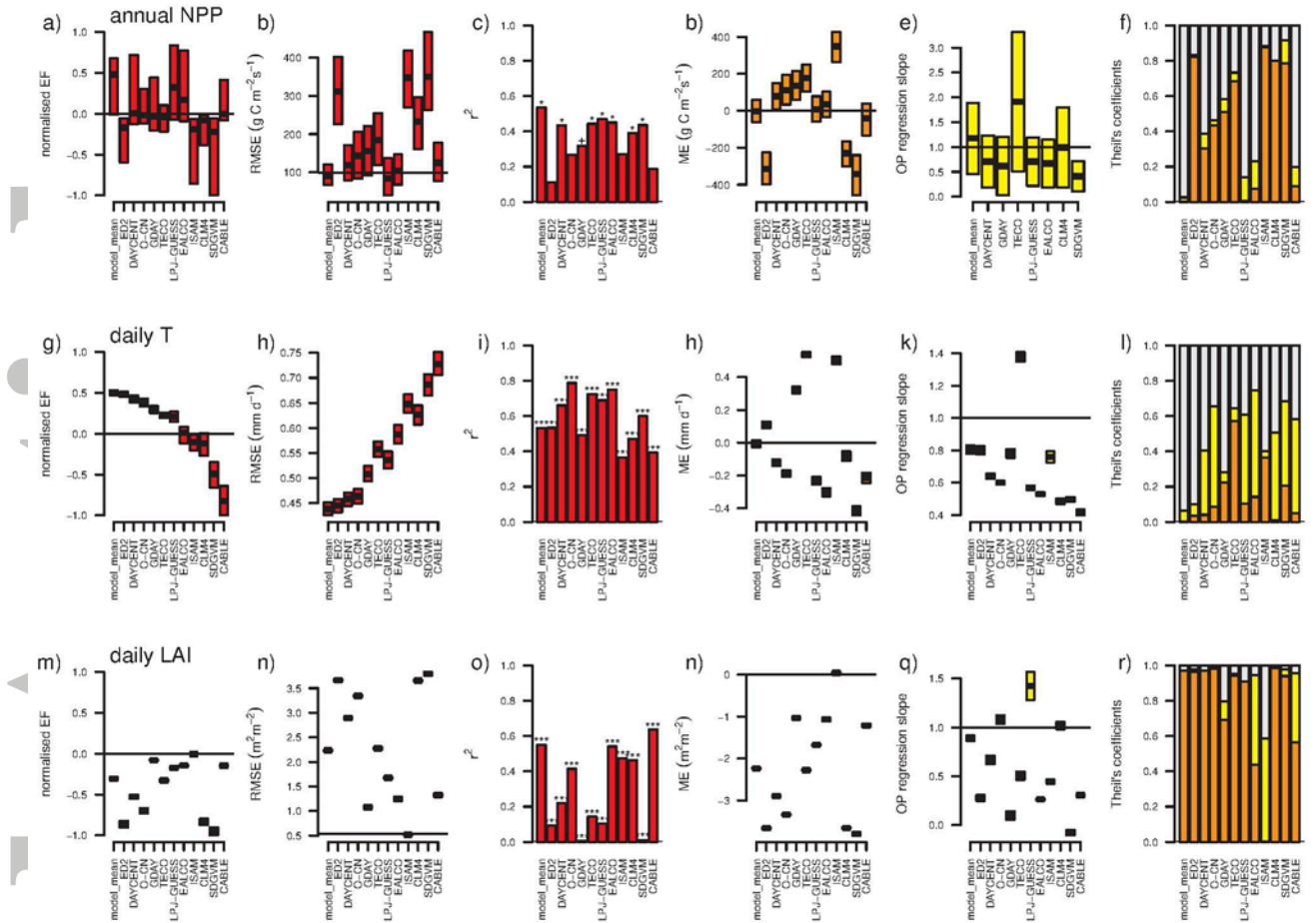


Figure 4. Goodness-Of-Fit (GOF) measures for all models and multi model mean at reproducing ambient  $\text{CO}_2$  annual NPP (a-f), daily transpiration (g-l) and daily LAI (m-r, pine only LAI) at Duke. GOF statistics are model efficiency (EF), root mean square error (RMSE), coefficient of determination ( $r^2$ ), mean error (ME), slope bias (slope) and Theil's coefficients. Negative EF values were normalised by dividing by the most negative EF value. The horizontal line on the RMSE plots indicate the mean over time of the observed 95% confidence interval. Note that observed values were regressed on predicted values so a positive magnitude bias indicates a negative model bias and a sensitivity bias  $>1$  indicates that the model was under-sensitive to drivers of inter-annual variability in the observations. Theil's coefficients assign the proportion of model error accounted for by mean error (ME; orange), slope bias (slope; yellow) and non-systematic error (grey).



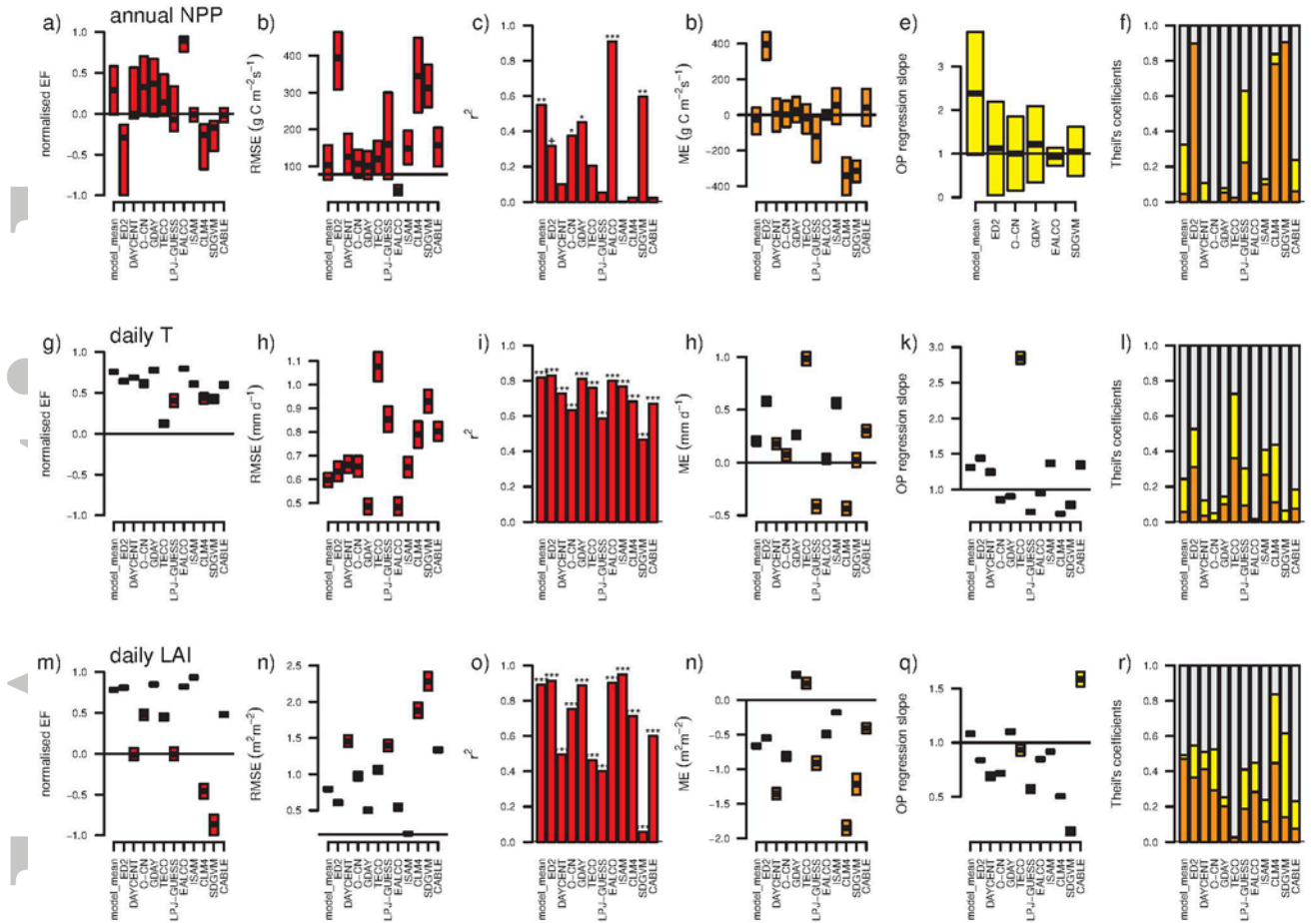


Figure 5. Goodness-Of-Fit (GOF) measures for annual NPP, daily transpiration and daily LAI at Oak Ridge. See Figure 4 caption for details.

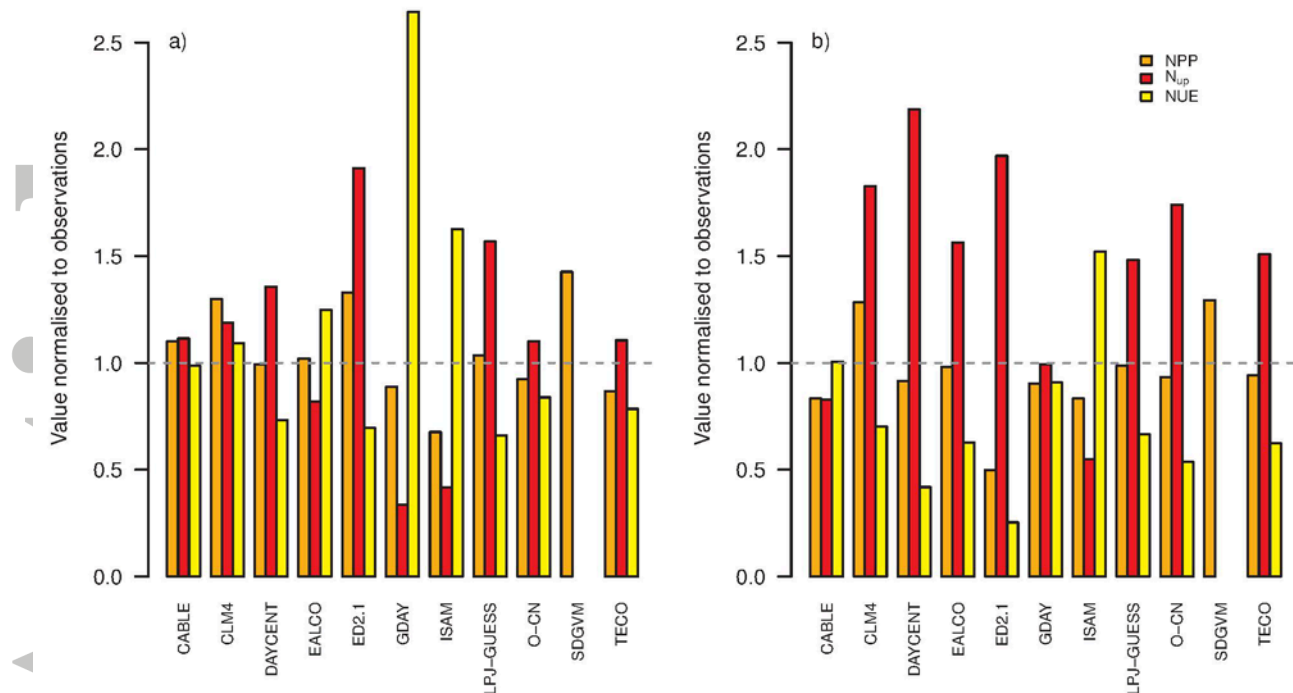


Figure 6. Simulated mean annual Net Primary Production (NPP; orange), nitrogen uptake ( $N_{up}$ ; red) and nitrogen use efficiency ( $NPP/N_{up}$ ; yellow) for 1998 to 2005 at Duke (a) and for 1999 to 2008 at Oak Ridge (b). All data are normalised by the observed mean values for the same averaging period.

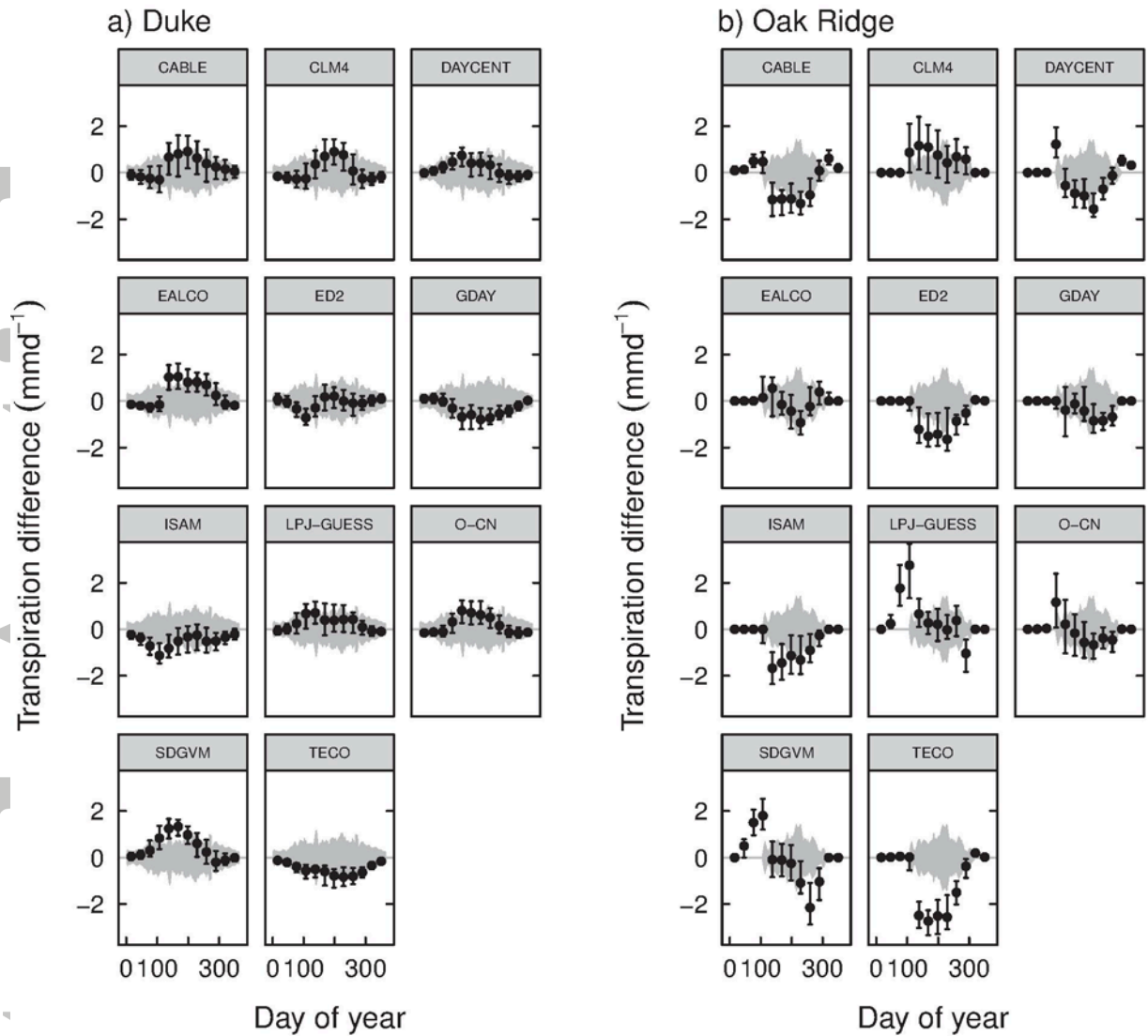


Figure 7. The difference between modelled transpiration and observed transpiration at Duke (1998–2007; a) and Oak Ridge (1999, 2004, 2007 and 2008; b). Monthly mean difference (points) and inter-quartile-range of the difference (error bars).. Grey shaded area represents the 95% CI of the observations.

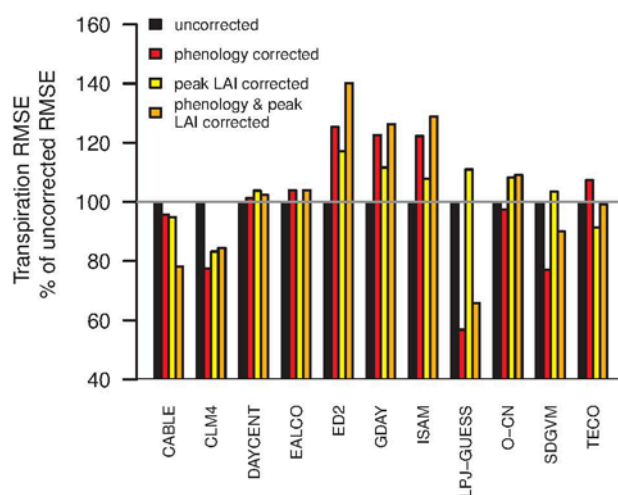


Figure 8. Root mean square error in daily transpiration predictions at Oak Ridge, uncorrected (black bars), corrected for phenology bias (red bars), corrected for maximum LAI bias (yellow bars) and corrected for both phenology and maximum LAI (orange bars); absolute values (a) and percentage of uncorrected RMSE (b). RMSE values are normalised to the uncorrected value.

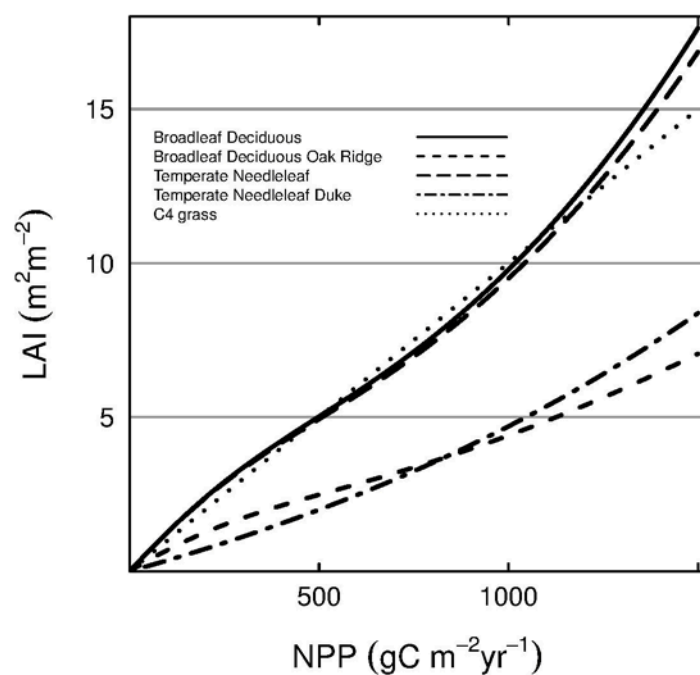


Figure 9. LAI as a function of NPP as hypothesised by CLM4, parameterised for the default and Oak Ridge broadleaf deciduous PFTs, the default and Duke temperate evergreen needleleaf PFTs and C4 grasses.