

CO₂ fertilization in temperate FACE experiments not representative of boreal and tropical forests

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Abstract

Results from free-air CO₂ enrichment (FACE) experiments in temperate climates indicate that the response of forest net primary productivity (NPP) to elevated CO₂ might be highly conserved across a broad range of productivities. In this study, we show that the LPJ-GUESS dynamic vegetation model reproduces the magnitude of the NPP enhancement at temperate forest FACE experiments. A global application of the model suggests that the response found in the experiments might also be representative of the average response of forests globally. However, the predicted NPP enhancement in tropical forests is more than twice as high as in boreal forests, suggesting that currently available FACE results are not applicable to these ecosystems. The modeled geographic pattern is to a large extent driven by the temperature dependence of the relative affinities of the primary assimilation enzyme (Rubisco) for CO₂ and O₂.

Keywords: carbon cycle, climate change, CO₂ fertilization, ecosystem model, FACE, forest response, LPJ-GUESS, NPP, photosynthesis, Rubisco

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Introduction

Increasing atmospheric CO₂ is one of the most important global change drivers, not only as an agent of greenhouse forcing but also as a limiting resource for carbon assimilation by plants (Farquhar *et al.*, 1980). Numerous small-scale greenhouse or open-top chamber experiments have shown that an increase in CO₂ concentrations of about 300 ppmv enhances photosynthesis in C₃ plants on the order of 60%, leading to substantial, although more variable, increases in net primary productivity (NPP; for reviews, see Curtis & Wang, 1998; Norby *et al.*, 1999). However, the applicability of such results to real ecosystems has been questioned (Norby *et al.*, 1999). Free-air CO₂ enrichment (FACE) technology was developed in order to overcome the recognized problems of smaller scale experiments (Hendrey *et al.*, 1999; Norby *et al.*, 1999). FACE results generally confirm

the enhancement of NPP by elevated CO₂ (Nowak *et al.*, 2004; Ainsworth & Long, 2005; Norby *et al.*, 2005). After analyzing the results from the longest running forest FACE experiments, Norby *et al.* (2005) concluded that '... the response of forest NPP is highly conserved across a wide range of productivity, with a stimulation at the median of 23 ± 2%' (for approximately 550 ppmv CO₂).

Studies with large-scale ecosystem models, which simulate physiological CO₂ effects based on the biochemical processes underlying carbon assimilation, have suggested that CO₂ 'fertilization' could be having a substantial impact on global NPP (Melillo *et al.*, 1993; Cramer *et al.*, 2001). The positive effects of increasing CO₂ might also be a major driver of the land carbon sink during the 1980s and 1990s (Prentice *et al.*, 2001). The magnitude of these modeled CO₂ effects has been contested; however (e.g. Hungate *et al.*, 2003), especially as models tend to predict a still larger NPP enhancement with a continuing CO₂ rise into the future (Pan *et al.*, 1998; Cramer *et al.*, 2001; McGuire *et al.*, 2001; Bachelet *et al.*, 2003). A necessary test for models is therefore to evaluate the magnitude of their response to the same CO₂ enhancement as applied in FACE experiments.

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In this study, we compared the response of forest NPP that is predicted by the dynamic vegetation model LPJ-GUESS (Smith *et al.*, 2001) to the results from FACE experiments, as summarized by Norby *et al.* (2005). We also carried out a global forest FACE experiment and analyzed geographic differences in the predicted CO₂ response of forests, including climate regions for which no experimental data are available. We restricted our study to forest ecosystems, as these have the largest potential of influencing the global carbon cycle (Bousquet *et al.*, 2000; Prentice *et al.*, 2001).

Material and methods

LPJ-GUESS

LPJ-GUESS (Smith *et al.*, 2001; Hickler *et al.*, 2004) is a generalized, process-based model of vegetation dynamics and biogeochemistry designed for regional to global applications. It combines features of the widely used Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ-DGVM; Sitch *et al.*, 2003) with those of the General Ecosystem Simulator (GUESS; Smith *et al.*, 2001) in a single, flexible modeling framework. The models have identical representations of ecophysiological and biogeochemical processes, including the hydrological cycle updates described in Gerten *et al.* (2004) and disturbance by wildfires (Thonicke *et al.*, 2001). They differ in the level of detail with which vegetation dynamics and canopy structure are simulated: simplified but computationally efficient representations are used in the LPJ-DGVM, while in GUESS, a more detailed and mechanistic approach, distinguishing individual and population structure and patch-scale heterogeneity, is used. Model representations of stochastic establishment, individual tree mortality, and disturbance events in GUESS are based on the FORSKA2 forest gap model (Prentice *et al.*, 1993). In order to represent regional vegetation, a number of replicate patches (here 50) are simulated, and the average is taken to represent the vegetation at a stand to landscape scale.

Physiological processes (e.g. photosynthesis, plant respiration, and microbial decomposition) and associated fluxes of carbon and water between soil layers, vegetation, and the atmosphere in LPJ-GUESS are simulated on a daily time step. Growth and vegetation dynamics are updated by allocating the annually accrued NPP to leaves, sapwood, and fine roots in conformity with a set of allometric rules (Sitch *et al.*, 2003). Sapwood-to-heartwood conversion, litterfall, fine root turnover, establishment, mortality, and disturbance are all simulated annually. Vegetation is represented as a mixture of plant functional types (PFTs), which are

differentiated by bioclimatic limits and physiological, morphological, phenological, and life history criteria governing competition for light and water. The model is driven by daily values of temperature, precipitation, and percentage sunshine hours, information on latitude, and soil texture, and a global atmospheric CO₂ concentration value.

A modified Farquhar photosynthesis scheme (Collatz *et al.*, 1991; Haxeltine & Prentice, 1996a,b) calculates vertically integrated canopy photosynthesis analytically as a function of absorbed photosynthetically active radiation, temperature, and atmospheric CO₂ concentration, under the assumption of optimal nitrogen allocation to leaves at different levels in the canopy (Haxeltine & Prentice, 1996a). If the water supply, which is determined by plant root-weighted soil moisture availability and maximum sapflow rates, is lower than the atmospheric demand, which is calculated based upon the leaf conductance associated with an unstressed photosynthesis rate, canopy conductance is reduced until transpiration equals the supply. Under these circumstances, the diffusion of CO₂ into the leaf is also decreased, resulting in lower photosynthesis rates.

In this study, a generic patch-destroying disturbance regime, representing stochastic events such as windstorms and pest outbreaks, was applied with a mean disturbance interval of 100 years. The set of PFTs in the LPJ-DGVM was enhanced by subdividing each PFT into shade-tolerance classes (Smith *et al.*, 2001; Hickler *et al.*, 2004). Vegetation dynamics parameters were re-calibrated using data on pristine forest vegetation dynamics, composition, and structure in different biomes (P. Miller & T. Hickler, unpublished results).

LPJ-GUESS and the closely related LPJ-DGVM have been evaluated by comparison with observations in a large number of studies (<http://www.pik-potsdam.de/lpj>). Output variables evaluated include NPP (e.g. Zaehle *et al.*, 2005; Hickler *et al.*, 2006), stand-scale and continental-scale evapotranspiration (AET) and runoff (Gerten *et al.*, 2004), vegetation greening trends in high northern latitudes (Lucht *et al.*, 2002) and the African Sahel (Hickler *et al.*, 2005), stand-scale leaf area index (LAI) and gross primary productivity (GPP; Arneth *et al.*, 2007), and forest stand structure and development (Smith *et al.*, 2001; Hickler *et al.*, 2004).

Model experiments

We evaluated the model through a site-by-site comparison with FACE experiments, and by carrying out a 'global forest FACE experiment' with the model.

For four FACE experiments [the same as in Norby *et al.* (2005); Table A1], the model was run with site-specific meteorological data (temperature, precipitation,

and incoming shortwave radiation), as well as information on soil texture, CO₂ concentration in the atmosphere, and vegetation structure and composition. Meteorological data were obtained through site home pages [FACTS II (<http://www.fs.fed.us/nc/face> (date of access: April 2004)), ORNL (<http://public.ornl.gov/face/ORNL> (date of access: April 2004))] or directly from researchers working at the sites. The climate input consisted of daily fields, except for FACTS I, where daily values were derived by linear interpolation between monthly average values. As site-specific meteorological data were only available during the course of the CO₂ experiments, a gridded global climate dataset (CRU TS 2.1; Mitchell & Jones, 2005), was used for the period of forest growth before CO₂ elevation began. For this period, daily values were derived by linear interpolation between the monthly means.

The choice of years for the data-model intercomparison (Fig. 1) was constrained by the availability of meteorological data at the time of the modeling experiments and published NPP estimates. The years used in this study are therefore not identical to those included by Norby *et al.* (2005), who only used data from the years after canopy closure. Using this criterion, Norby *et al.* (2005) excluded the years that we used at FACTS II, and the first 2 years of data that we used for ORNL.

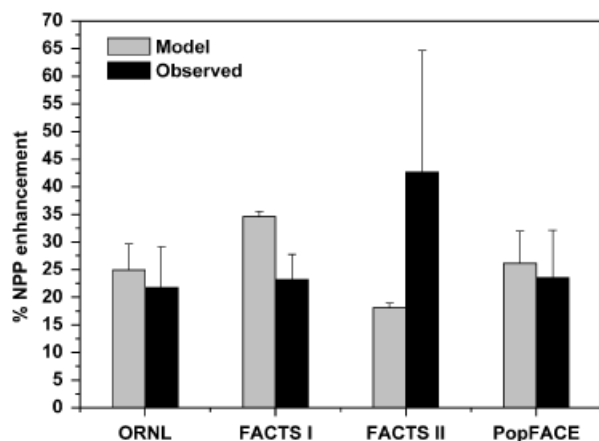


Fig. 1 Simulated vs. observed annual NPP enhancement (mean and 95% confidence intervals) under elevated CO₂ for four FACE sites, averaged over the period for which station climate and NPP data were available: 1999–2002 for ORNL (Oak Ridge National Laboratory), temperate broad-leaved forest (observed NPP from Norby *et al.*, 2002, 2003); 1998–2000 for FACTS I (forest atmosphere carbon transfer and storage I), North Carolina, temperate needle-leaved forest (Schäfer *et al.*, 2003); 1999–2001 for FACTS II, Wisconsin, boreal broad-leaved forest (King *et al.*, 2005); 2000–2001 for PopFACE, Italy, broad-leaved coppice plantation (Gielen *et al.*, 2005). At the PopFACE site, data from different species (Table A1) were used as independent data points for calculating the confidence interval ($N = 6$).

Modeled and observed vegetation structure and composition are given in Table A1. The growing conditions at the FACE sites (monocultures with a certain planting density and stand age) were prescribed in the model (Table A1), and further establishment was disabled up to and during the period of CO₂ enhancement. In the case of the two older stands (FACTS 1 and ORNL), the model was run with the standard model representations of natural tree mortality. Mortality was switched off for the FACTS II and PopFACE site, because the stands are only a few years old and substantial mortality has not occurred. LAI was allowed to respond to CO₂, even if the experimental data do not suggest LAI changes.

The tree species planted at the FACE sites are not explicitly parameterized in the model and were represented by the corresponding PFT (Table A2). The main differences between the PFTs at the four different sites concern phenology (evergreen vs. deciduous), leaf or needle form (e.g. specific leaf area), and climatic distribution (boreal vs. temperate), whereby boreal types have a lower optimum temperature for photosynthesis (Smith *et al.*, 2001) and higher base respiration rates. More information on PFT parameterization is given in Table A3.

At FACTS II, model results were compared with the observed response of pure trembling aspen (*Populus tremuloides*) stands, because differences in the strength of intra-specific and inter-specific competition might influence the observed CO₂ response (King *et al.*, 2005).

At the PopFACE site, irrigation (Calfapietra *et al.*, 2003) was implemented within the model by increasing daily precipitation until it matched the modeled daily potential evapotranspiration (PET; Haxeltine & Prentice, 1996b), if PET was larger than rainfall during the growing season (mean daily temperature above 5 °C). Model results were only compared with the results from the first rotation period (Calfapietra *et al.*, 2003). Plant allometric relationships and thereby growing conditions during the second rotation, when a developed root system was in place from the first rotation period (Liberloo *et al.*, 2006), are not represented in the model in its current form.

The generalized parameterization of the model was not adapted to site conditions, with the exception of the leaf area to sapwood cross-sectional area ratio of the PFT representing *Pinus taeda* at FACTS I (Table A3). Without more site-specific and species-specific calibration, which is beyond the scope of this study, we would not expect the model to reproduce details in the observed variation of CO₂ responses. However, the results of the global FACE experiment can only be regarded realistic if the model reproduces the general magnitude of the NPP response to elevated CO₂.

The global model experiment was carried out using the gridded CRU TS 2.1 global climate dataset (Mitchell & Jones, 2005), and gridded information on soil texture (Sitch *et al.*, 2003). Two runs were carried out: one with actual historical CO₂ concentrations from 1901 to 2002 [McGuire *et al.*, 2001; TRENDS (<http://cdiac.esd.ornl.gov/trends/co2/contents.htm>)], and one with historical CO₂ concentrations increased to 550 ppmv during 1996–2002. The latter 6-year period was chosen for analysis of the model results, as it would represent climatic conditions similar to those prevailing during the period when most of the FACE data were obtained. The model was run with potential natural vegetation and for all grid cells that would naturally carry forests (Haxeltine & Prentice, 1996b), with the exception of tropical deciduous forests, which have a savanna-like structure. Following a 300-year spin-up to establish the 'steady-state' vegetation, the model was driven by the observed climate from 1901 to 2002.

Results

Modeled and observed NPP responses to elevated CO₂ may be compared in Fig. 1. Averaged over all sites, NPP was increased by 27.8% ($\pm 10.0\%$; $N = 4$) according to the FACE data, and the model predicted a 25.9% ($\pm 6.8\%$; $N = 4$) increase in NPP. However, at FACTS I, the modeled response was 10.3% higher than that observed in absolute terms (corresponding with an overestimation by 49%), while at FACTS II, the modeled response was 24.6% lower than the observed one (Fig. 1).

Table 1 compares the CO₂ response of forest NPP to elevated CO₂ indicated by Norby *et al.* (2005) to the response predicted by the model, averaged over all areas of the globe that are potentially forested, and for different biomes. The modeled global average response

Table 1 Modeled NPP response (averages over 1996–2002 and 95% confidence intervals) as predicted for all forests globally and for different biomes, compared with the response of forest NPP suggested by Norby *et al.* (2005)

| | NPP enhancement (%) | <i>N</i> |
|----------------------------|---------------------|----------|
| Norby <i>et al.</i> (2005) | 23 \pm 2 | 19 |
| Global forests | 24.5 \pm 0.06 | 130 571 |
| Boreal forests | 15.1 \pm 0.06 | 77 159 |
| Temperate forests | 25.7 \pm 0.14 | 22 974 |
| Tropical forests | 35.1 \pm 0.09 | 30 439 |

For calculating confidence intervals (two times the standard error of the sample mean), different years of data or modeled response for the same site or grid cell were treated as independent data points.

was within the confidence interval of the estimate by Norby *et al.* (2005), based on four FACE forests. The modeled average response for temperate forests was 2.7% higher than that suggested by Norby *et al.* (2005). More strikingly, the modeled response in tropical forests was more than twice as high as the response predicted for boreal forests.

Figure 2 shows the geographical pattern of the modeled NPP enhancement in response to elevated CO₂. The NPP enhancement was predicted to generally increase toward the equator. The strongest response was predicted for warm temperate and tropical forests. Geographic variations in the NPP response [Δ NPP (%)] were largely associated with differences in temperature, linear regression analysis yielding $R^2 = 0.67$ (Fig. A1a). Water availability, expressed as the ratio of actual to potential evapotranspiration (AET/PET) for ambient CO₂ concentrations, was also significantly related to Δ NPP, but only with $R^2 = 0.11$ (Fig. A1b). The residuals from the regression with temperature were only weakly related to AET/PET ($R^2 = 0.01$), with a stronger NPP response under drier conditions. Because of the large sample size (21 762 global forest grid cells), all regressions are highly significant ($P < 0.001$), but model results based on interpolated gridded spatial climate datasets as here are spatially highly auto-correlated, making the *P*-value meaningless.

Grid cells for which the model predicted very low NPP ($0.1 \text{ kg m}^{-2} \text{ yr}^{-1}$) and grid cells for which the model did not predict forest biomes (woody LAI < 0.5 for boreal forests and 2.5 for the remaining forests; Haxeltine & Prentice, 1996b) were excluded. These restrictions had only a very minor effect on the presented results.

Discussion

The model reproduced the overall response of forest productivity to elevated CO₂ observed in FACE experiments. We regard this as a requirement for any ecosystem model that is to be applied for simulating future ecosystem dynamics under rising levels of CO₂. Part of the discrepancies between the modeled and observed response at individual sites might be explained by the fact that the model parameterization was not explicitly adapted for all site-specific conditions that might influence the response to elevated CO₂; for example, the actual planted tree species. The number of sites, however, is too small to draw conclusions as to the general ability of the model to capture between-site variations in response to CO₂. In the case of FACTS I, the model might have overestimated the response, because nutrient limitations, which are not explicitly represented in the model, might limit the NPP enhancement under

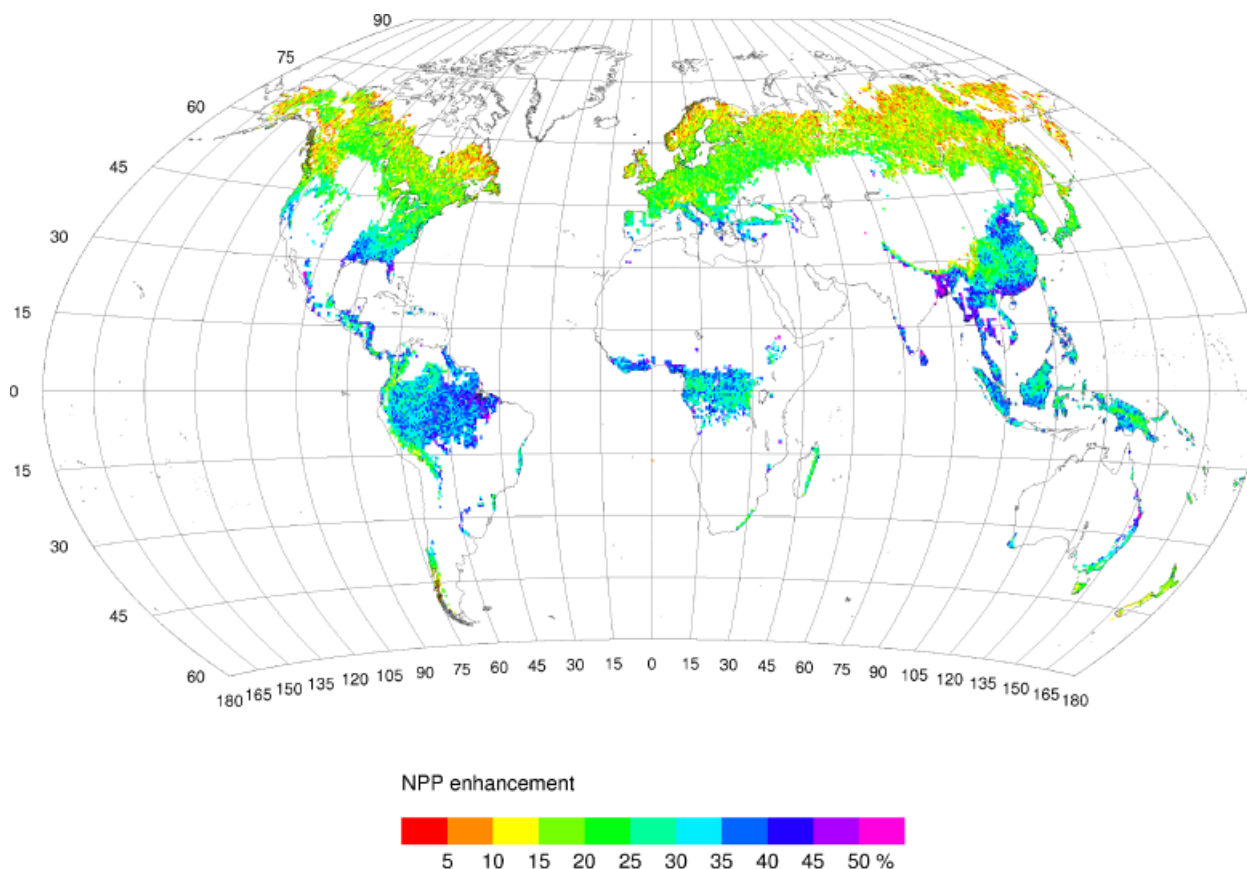


Fig. 2 Geographic pattern of the simulated NPP enhancement, resulting from a step increase of CO₂ from ambient to 550 ppmv; NPP values averaged over 1996–2002.

elevated CO₂ (Oren *et al.*, 2001; Finzi *et al.*, 2002, 2006; McCarthy *et al.*, 2006). At the FACTS II site, the reasons for the mismatch are less clear. King *et al.* (2005) speculated that the response at this site might be particularly strong, because the recently weathered soils may be high in nutrients, compared with many temperate forests, and because competition for light is less intense in the relatively open canopy. The observed NPP enhancement increased from 29% in 1999 to 64% in 2001 (King *et al.*, 2005; Table 3), while the modeled response was rather constant over the same period. This indicates that the model might not capture the growth conditions in this young forest plantation, possibly because LAI and NPP are overestimated (Table A1).

Geographic variations

The model predicted that CO₂ effects on NPP differ between biomes (Table 1; Fig. 2). Climate change is likely to increase NPP more in cold northern regions than close to the equator because of a greater proportional growing season extension in temperature-limited environments (Rustad *et al.*, 2001; Morales *et al.*, 2007).

The results of this study suggest that the direct CO₂ response of NPP, by contrast, will be stronger in warm regions.

Regional differences in the modeled CO₂ response were to a large extent driven by the temperature response of the relative affinity of the carboxylation enzyme Rubisco for CO₂ and O₂. Increased temperatures lead to an increased relative fixation of O₂ (oxygenation), leading to photorespiration, an energy-dependent process that reduces net photosynthesis (Jordan & Ogren, 1984). Using the models of Farquhar *et al.* (1980) and Farquhar & von Caemmerer (1982), Long (1991) showed that this effect causes a much stronger CO₂ enhancement of photosynthesis at high temperatures than at low temperatures. According to the model, an increase in atmospheric CO₂ from 350 to 650 $\mu\text{mol mol}^{-1}$ could increase light-saturated CO₂ uptake by 20% at 10 °C and by 105% at 35 °C. The version of the Farquhar model which is implemented within LPJ-GUESS likewise predicts such a strong temperature dependence of the photosynthetic response on elevated CO₂ (Fig. A2). Kirschbaum (1994) coupled a simplified version of the Farquhar model to a model of stomatal

conductance and predicted a similar geographic pattern in response of photosynthesis to elevated CO₂ as found for NPP in the present study. Thus, there exists a strong physiological basis for a temperature dependence of NPP responses on elevated CO₂.

LPJ-GUESS tends to simulate a stronger response to CO₂ under drier conditions, because elevated CO₂ reduces the negative effects of drought on plant growth (Gerten *et al.*, 2005), which has limited support by the available data (Wullschleger *et al.*, 2002; Nowak *et al.*, 2004). Temperature, however, is a stronger driving force in the model.

Interactions between temperature and CO₂ have recently received considerable attention in the literature, but no quantitative conclusions have been drawn (Norby & Luo, 2004), perhaps because of a paucity of unequivocal data from field experiments (Morison & Lawlor, 1999; Norby & Luo, 2004). In this regard, it may be unfortunate that current long-running forest FACE experiments are all located in the temperate zone and hence subject to a limited range of growing season temperatures. Manipulating air temperature in forests is difficult, and therefore most forest data with multiple temperature treatments come from soil warming experiments or from small numbers of young trees (Norby & Luo, 2004). Furthermore, very few experiments have addressed growth stimulation by CO₂ at temperatures below 10 °C (Morison & Lawlor, 1999), which can prevail during a significant part of the growing season in cold temperate and boreal forests. The predicted weakness of CO₂ effects at low temperatures might partly explain why rather small CO₂ effects have been found in high alpine (Körner *et al.*, 1996) and arctic (Tissue & Oechel, 1987) ecosystems.

Long-term responses

It remains to be seen whether the strong medium-term responses observed in FACE experiments will be maintained in the longer term, and if the results obtained in young plantations also apply to mature forests (Körner, 2000). It has been argued that nutrient limitations (especially N) will constrain NPP responses in the future (Finzi *et al.*, 2002; Hungate *et al.*, 2003), but to date there is no unambiguous evidence for a general effect of this kind (Finzi *et al.*, 2006; Norby & Iversen, 2006). In the FACTS I experiment, for example, elevated CO₂ has now increased basal area increment (BAI) by 13–27% for 8 years, with no reduction over time (Moore *et al.*, 2006), even though the response might have been even stronger in the absence of nutrient limitation (Oren *et al.*, 2001). Finzi *et al.* (2007) showed that at FACTS I, FACTS II, and ORNL, N uptake rates were increased under elevated CO₂, which could be one reason for the

prolonged NPP enhancement in spite of strong nutrient limitation at FACTS I and ORNL.

Regarding the applicability of FACE results from young plantations to mature forests, Körner *et al.* (2005) and Asshoff *et al.* (2006) did not find significant increases in BAI in a mature deciduous forest in Switzerland. However, the photosynthetic response was similar to that of younger stands (Zotz *et al.*, 2005), only a small number of adult trees were measured, and NPP was not estimated. McCarthy *et al.* (2006) showed that NPP responses at FACTS I were mainly controlled by changes in LAI, with no NPP effect after canopy closure for a given LAI, but further experiments are necessary to establish the generality of this result. One also has to keep in mind that most forests are not mature, being constantly altered by humans or natural disturbances (e.g. Botkin & Simpson, 1990). In summary, current evidence does not preclude the possibility that strong long-term future impacts of increasing CO₂ on NPP and carbon storage, as predicted by the LPJ model in a number of studies (e.g. Cramer *et al.*, 2001; Bachelet *et al.*, 2003), might be realistic.

Final remarks

This study clearly demonstrates the benefits arising from the combination of experimental work and modeling. Process-based models such as LPJ-GUESS are primarily based upon mechanistic understanding of ecosystem processes, such as photosynthesis and autotrophic respiration, which has largely been obtained through experimental work at small scales. Outcomes of modeling studies can be independently tested against results from ecosystem scale experiments and, if the test is successful, can be used to extrapolate beyond the unavoidably limited environmental space of the experiments. Process-based ecosystem models can include the effects of simultaneous variations in multiple environmental drivers, which can rarely be investigated in ecosystem experiments (Norby & Luo, 2004), but they can also be used to distinguish the effects of individual drivers (Lucht *et al.*, 2002; Hickler *et al.*, 2005). In this study, the model has generated a hypothesis about the magnitude of the CO₂ response in different climatic regions, which can be tested by applying FACE methodology in tropical and boreal forests. Factors, which are not explicitly represented by the model, such as nutrient limitations, might lead to a different geographical pattern.

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Appendix A

Table A1 Modeled and observed FACE site characteristics

| | ORNL | FACTS I | FACTS II | PopFACE |
|--|--|---|---|---|
| Location | Oak Ridge, Tennessee, USA | Durham, North Carolina, USA | Rhineland, Wisconsin, USA | Toscana (Viterbo), Italy |
| Latitude, longitude | 35°54'N, 84°20'W | 35°58'N, 79°05'W | 45°40'N, 89°37'N | 42°22'N, 11°48'E |
| Observed LAI* | 5.1 | 3.4 | 2.7–3.4 | 4.6–7.4 |
| Modeled LAI† | 4.4 | 2.8 | 3.4 | 7.7 |
| Observed biomass (g C m ⁻²) | 5921‡ | 5394§ | ~800†¶ | 749 |
| Modeled biomass (g C m ⁻²) | 2080‡ | 4200§ | 1049† | 2164 |
| Observed NPP (g C m ⁻² yr ⁻¹)†** | 994 (86) | 891 (252) | 330 (70) | 1451 (257††) |
| Modeled NPP (g C m ⁻² yr ⁻¹)†** | 758 (94) | 778 (15) | 671 (96) | 1125 (381) |
| Main species | <i>Liquidambar styraciflua</i> L. | <i>Pinus taeda</i> L. | <i>Populus tremuloides</i> Michx. | <i>Populus alba</i> L., <i>P. nigra</i> L., <i>P. × euramericana</i> Dode Gunier |
| Model PFT | Temperate, intermediate shade-tolerant, broad- leaved tree | Temperate, intermediate shade-tolerant, needle- leaved tree | Boreal, shade- intolerant, broad- leaved tree | Temperate, shade-intolerant, broad-leaved tree |
| Plantation year | 1988 | 1983 | 1997 | 1999 |
| Sapling density (per hectare) | 3600 | 1700 | 10 000 | 10 000 |
| Elevated CO ₂ concentration (ppmv) | 550 | 580 | 580 | 550 |

*LAI, leaf area index; data from Norby *et al.* (2005).

†Value for ambient CO₂, averaged for all years used in the data-model intercomparison (Fig. 1).

‡Value for ambient CO₂ for the year 1998 (http://public.ornl.gov/face/synthesis/N_Synthesis-CDIAC.htm).

§Value for ambient CO₂ for the year 1998, excluding hardwoods (Hamilton *et al.*, 2002).

¶King *et al.* (2005; Fig. 1).

||Value for 2001, averaged for three *Populus* species (Calfapietra *et al.*, 2003).

**Values only for ambient CO₂, confidence intervals (treating each year as one measurement) given in parentheses.

††Data from the three *Populus* species and 2 years treated as independent data points (*N* = 6).

Table A2 Set of plant functional types (PFTs) in the LPJ-DGVM (Sitch *et al.*, 2003) was enhanced by subdividing each PFT into shade-tolerance classes (Smith *et al.*, 2001; Hickler *et al.*, 2004), resulting into the following list of PFTs

| PFT | Examples of typical taxa |
|---|---|
| Tropical, shade-tolerant, broad-leaved, evergreen tree | |
| Tropical, shade-intolerant, broad-leaved, evergreen tree | |
| Tropical, intermediate shade-tolerant, broad-leaved, rain-green tree | |
| Temperate, shade-tolerant, broad-leaved, deciduous tree | <i>Fagus</i> |
| Temperate, intermediate shade-tolerant, broad-leaved, deciduous tree | <i>Quercus</i> , <i>Tilia</i> , <i>Fraxinus</i> |
| Temperate, shade-intolerant, broad-leaved, deciduous tree | <i>Betula</i> , <i>Populus</i> |
| Temperate, intermediate shade-tolerant, needle-leaved, evergreen tree | <i>Pinus</i> |
| Temperate, intermediate shade-tolerant, broad-leaved, evergreen tree | <i>Quercus</i> |
| Boreal, shade-tolerant, needle-leaved, evergreen tree | <i>Picea</i> |

Continued

Table A2. (Contd.)

| PFT | Examples of typical taxa |
|--|--------------------------|
| Boreal, intermediate shade-tolerant, needle-leaved, evergreen tree | <i>Pinus, Abies</i> |
| Boreal, shade-intolerant, broad-leaved, deciduous tree | <i>Betula, Populus</i> |
| Boreal, shade-intolerant, needle-leaved, deciduous tree | <i>Larix</i> |
| Herbaceous with C ₃ photosynthesis | |
| Herbaceous with C ₄ photosynthesis | |

Table A3 PFTs (Table A2) were distinguished by the following parameters (Smith *et al.*, 2001)

| Leaf morphology | Needle-leaved | Broad-leaved | |
|---|---------------|--------------|------------|
| Minimum canopy conductance (mm s ⁻¹) | 0.3 | 0.5 | |
| Leaf turnover rate (year ⁻¹) | 0.5* | 1.0 | |
| Fine root turnover rate (year ⁻¹)† | 0.7 | 0.7 | |
| Leaf to sapwood cross-sectional area ratio‡ | 3000 (1500§) | 4000 | |
| k _{allom1} ¶ | 150 | 200 | |
| Climatic range | Boreal | Temperate | Tropical |
| Optimal temperature range for photosynthesis (°C) | 10–25 | 15–25 | 20–30 |
| Tissue respiration rate at 10 °C (g C g N ⁻¹ day ⁻¹) | 0.122 | 0.066 | 0.011 |
| Shade tolerance | Tolerant | Intermediate | Intolerant |
| Sapwood to heartwood conversion rate (year ⁻¹) | 0.03 | 0.05 | 0.08 |
| Growth efficiency mortality parameter (g C m ⁻² yr ⁻¹)** | 90 | 100 | 110 |
| Maximum establishment rate (saplings yr ⁻¹ m ⁻²)†† | 0.05 | 0.1 | 0.15 |
| Minimum PAR at forest floor for establishment (MJ m ⁻² day ⁻¹) | 1.0 | 1.5 | 2.0 |
| Recruitment shape parameter‡‡ | 0.8 | 1.3 | 2.0 |

*With the exception of the boreal shade-intolerant needle-leaved tree (Table A2), which shed its leaves every year and therefore was assigned a leaf turnover rate of 0.5.

†In the original model version (Smith *et al.*, 2001), the root turnover rate was coupled with the leaf turnover rate. Here, one value was chosen for all PFTs, based on Vogt *et al.* (1996) and Li *et al.* (2003).

‡The original value of 8000 was replaced by lower values, following Martin *et al.* (1998), Becker *et al.* (1999), Eamus & Prior (2001), Tyree & Ewers (1991), McDowell *et al.* (2002).

§At the FACTS I site, a value of 1500 was used for *Pinus taeda*. This value is slightly higher than the values measured at the Duke forest by Naidu *et al.* (1998), which were approximately 1000, but using 1500 improved the modeled relationship between LAI and aboveground biomass.

¶k_{allom1} is an allometric parameter, determining the relationship between stem diameter and crown area [Sitch *et al.*, 2003; Eqn (4)]; a lower value implies smaller crowns for a given diameter.

||In LPJ-GUESS, different shade-tolerance classes are related to a number of parameters, which define a strategic trade-off: trees can either allocate to fast growth and high maximum recruitment; or to functions that permit survival at low growth rates resulting from intense shading by neighbors (Hickler *et al.*, 2004).

**Growth-efficiency-related mortality was modeled as an s-shaped function of the net primary productivity (NPP) of a tree cohort divided by its leaf area, averaged over the last 5 years (Prentice *et al.*, 1993). A growth efficiency mortality parameter (param_mort_{greff}) denotes the turning point of the curve defined by

$$\text{mort}_{\text{greff}} = 0.1 / (1 + (\text{greff}_{5\text{years}} / \text{param_mort}_{\text{greff}})^5),$$

where greff_{mort} represents the fraction of the cohort that will die, and greff_{5years} represents the growth efficiency over the last 5 years.

††Relative values, total maximum background establishment of all PFTs together was set to 0.3 saplings yr⁻¹ m⁻². Note that, for modeling of the FACE sites, establishment was prescribed (see 'Material and methods').

‡‡High values indicating strongly reduced establishment, as growth conditions at the forest floor become unfavorable as a result of low PAR levels (Fulton, 1991).

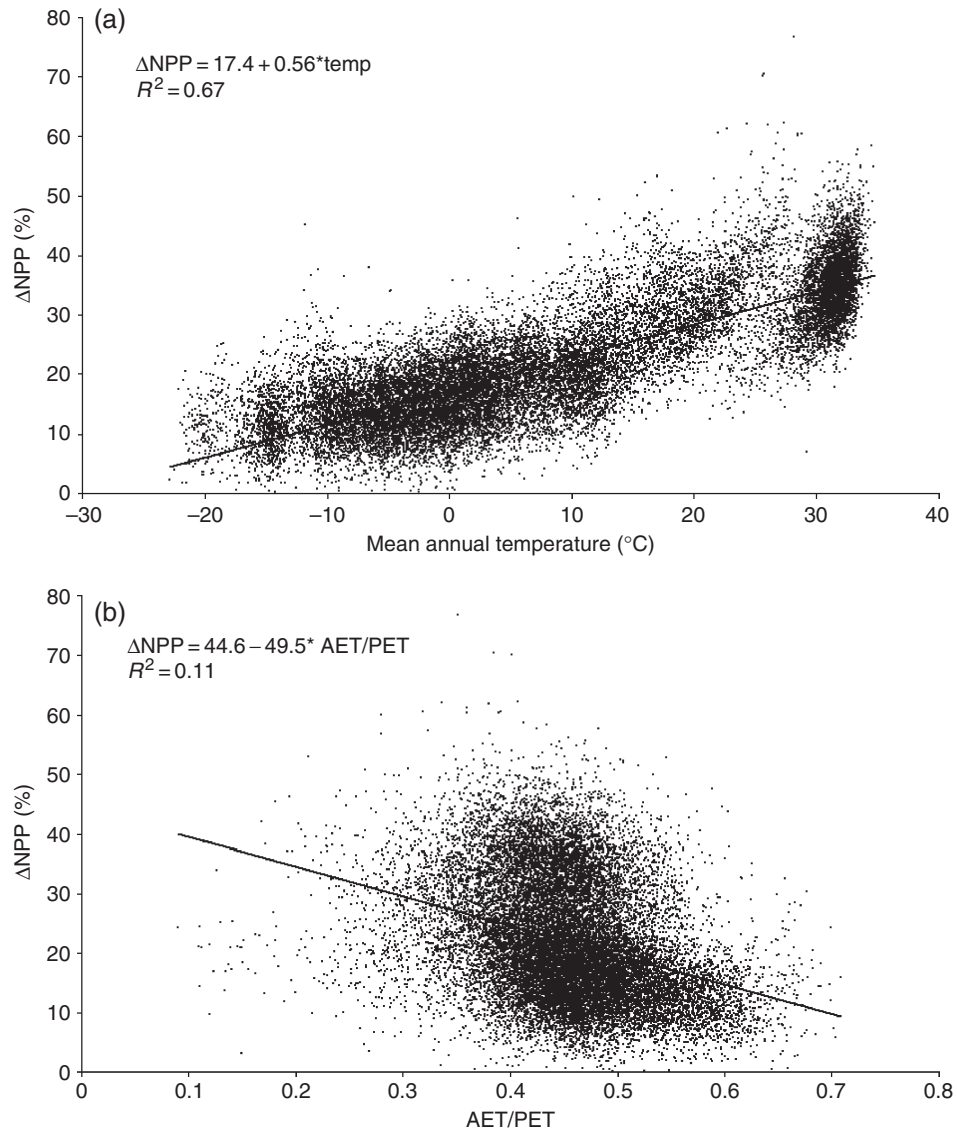


Fig. A1 Modeled relationship between NPP enhancement (ΔNPP) and environmental factors: (a) mean annual temperature; (b) mean annual actual/potential evapotranspiration (AET/PET). Values are averaged over 1996–2002.

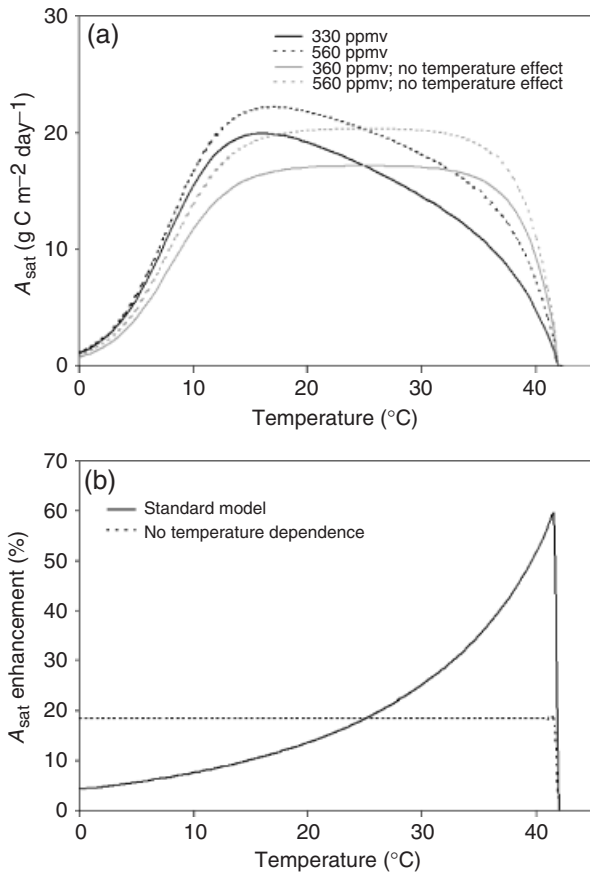


Fig. A2 Effects of elevated CO_2 and temperature on light-saturated gross daily photosynthesis (A_{sat}) of a temperate tree, as predicted by the photosynthesis module of LPJ-GUESS. The standard model is shown in black, and gray denotes the same simulations with k_c (Michaelis constant for Rubisco for CO_2), k_o (Michaelis constant of Rubisco for O_2), and τ (CO_2/O_2 specificity ratio) held constant at 25 $^{\circ}\text{C}$ values (i.e. no physiological temperature dependence; see Haxeltine & Prentice, 1996a for parameter values): (a) absolute values and (b) enhancement of A_{sat} in % if CO_2 is increased from 360 to 560 ppmv. At low temperatures and above a PFT-specific maximum temperature, photosynthesis is also inhibited by an empirical PFT-specific temperature-inhibition function (Sitch *et al.*, 2003). Day length was set to 12 h, and the photosynthetically active radiation (PAR) to $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

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