

Modelling CO₂ Impacts on Forest Productivity

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Abstract Process-based models are important tools for understanding the dynamics and functioning of forest ecosystems. In nearly all models, forest productivity is largely driven by carbon (C) input via photosynthesis, which reacts strongly positive to elevated CO₂ (eCO₂). The simulated increases in forest productivity in terms of wood production, however, have been much higher than experimental and observational evidence suggests, at least in those models that did not account for nutrient limitations. Experimental results show that in most investigated systems, eCO₂ leads to increasing allocation of C below ground, without sustained enhancements of wood production. This translocation of C below ground, which also enhances nutrient uptake, appears to be larger than simulated in our current models. However, because of a lack of experimental data from real ecosystems, in particular from the tropics, the big question remains unresolved whether increasing levels of CO₂ have and will lead to substantially increased forest productivity in terms of stand-level wood increment. To reduce the uncertainties, it will be necessary to develop new theory, implement that in models, and rigorously compare model results with observations. They range from physiological measurements, results from “free air CO₂ enrichment” experiments to forest inventories, tree rings and ¹³C analyses (as a proxy for changes in water use efficiency).

Key issues that should be addressed in the models include the coupling of C and nutrient cycles, limitations to the C sink capacity of trees, dynamic changes in allocation, and potential feedbacks from tree population dynamics on stand productivity.

Keywords Forest productivity · CO₂ fertilization · Net primary productivity (NPP) · Forest modelling · Allocation

Introduction

CO₂ is a limiting resource for photosynthesis [1–3]. CO₂ also affects leaf stomatal density [4] and stomatal conductance [5]. The direct effect on photosynthesis of increasing CO₂ is often referred to as “CO₂ fertilization,” which is more pronounced in plants with C₃ photosynthesis [3] because in plants with C₄ or CAM photosynthetic pathways, the CO₂ concentration around the enzyme catalyzing the carboxylation reaction is elevated by the plant and decoupled from the atmospheric concentration. All trees, however, are C₃ plants. Under elevated CO₂ (eCO₂), stomatal conductance generally decreases, which also leads to lower transpiration and water usage, whereby the decrease in transpiration also depends on how well leaves or needles are coupled to the atmosphere [6].

Photosynthesis of C₃ plants commonly increases nearly linearly up to leaf-internal CO₂ concentrations of about 200 parts per million (ppm). At higher concentrations, photosynthesis becomes increasingly limited by Ribulose biphosphate (RuBP) regeneration, and the CO₂ response curve levels off [7] (Fig. 1).

As photosynthesis is the primary entry point for all carbon (C) used by autotrophic life to synthesize carbohydrates and ultimately build biomass, understanding the effects of increasing levels of atmospheric CO₂ on photosynthesis is of utmost importance for predicting forest growth. The basic biogeochemistry of photosynthesis, including the direct CO₂ response under optimal conditions, is relatively well understood. However, it has been heavily debated how this response is modulated if growth conditions and the supply of other

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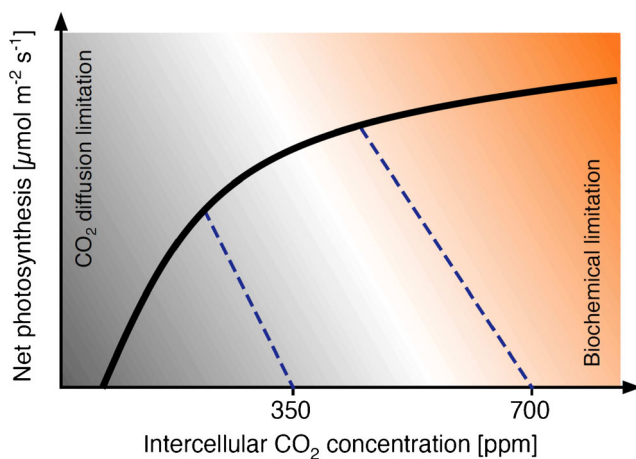


Fig. 1 Relationship between intercellular CO₂ concentration and net photosynthesis rate simulated with a simplified version of the Farquhar photosynthesis model [8], as modified by Farquhar and Caemmerer [9], fitted to leaf gas exchange measurements on snow gum (*Eucalyptus pauciflora*) [10]. C₃ plants generally show similar responses [7, 11]. The relationship to the atmospheric CO₂ concentration and the limitation by diffusion into the leaf is given by *dashed blue lines* for atmospheric CO₂ concentrations of 350 and 700 ppm, assuming a reduction of leaf conductance under future eCO₂. In summary, the CO₂ concentration in the atmosphere and diffusion into the leaf limits photosynthesis in the near-linear portion of the response curve, while RuBP regeneration increasingly limits photosynthesis at higher CO₂ concentrations [11]. The latter is sometimes referred to as biochemical limitation [11]

resources are limiting (e.g., [12–14]), and whether increased photosynthesis leads to enhanced forest productivity under those conditions [13, 15].

Other factors that might limit the extent to which plants can take advantage of increasing atmospheric CO₂ are environmentally imposed stress effects on the plant, e.g., as a result of very high temperatures, and other limiting resources, in particular nutrients and water. As these other factors might exert substantial limitations on photosynthesis and growth, it has been suggested that at current CO₂ levels, plants are generally no longer CO₂-limited [16].

Enhanced photosynthesis does not necessarily lead to increased forest productivity in terms of wood biomass production, primarily because plants might allocate the extra C to other functions than biomass growth, such as increased fine root production and turnover, root exudates and C transfer to mycorrhiza. The two latter processes each may utilize up to 30 % of assimilated C [11]. In a mature broad-leaved forest in Switzerland exposed to elevated CO₂ with free air CO₂ enrichment (FACE) technology, there was no significant enhancement of stem growth and leaf litter production, even though photosynthesis was persistently increased under eCO₂, suggesting increased C allocation below ground [15, 17]. Also at a highly nutrient-limited site in northern Sweden, eCO₂ in open-top chambers led to strong photosynthesis enhancements, but growth was only enhanced with optimum nutrient supply [18].

Forest models generally adopt one of two very different approaches for modelling productivity. (i) Empirically calibrated forest models commonly simulate a parameterized maximum productivity, expressed as biomass or stem diameter increment per year, which is modulated by environmental factors (soil conditions and climate, e.g., [19]). Such models cannot mechanistically represent the potential effects of changing CO₂ levels and are therefore not discussed any further in the following. (ii) “Process-based” forest models aim to represent the physiological processes and, in some cases, population dynamics that ultimately affect forest productivity. Forest productivity in such models thus emerges as the result of complex interactions between a variety of processes, such as photosynthesis, autotrophic respiration, and allocation of C to different tree compartments.

In this paper, we focus on the approaches for modelling CO₂ impacts on forest productivity in process-based forest and dynamic vegetation models, the results from these models up to date, and how well the model results correspond with available empirical evidence. We outline important shortcomings in current models and how the models could be improved.

Process-Based Models for Simulating Forest Productivity

Several types of process-based forest models are relevant for this review: forest stand simulators (e.g., 4C [20], BALANCE [21, 22]), forest succession models (e.g., ForClim [19]), ecosystem models or biogeochemistry models (e.g., BIOME-BGC [23], GOTILWA+ [24], PnET-CN [25]), and dynamic vegetation models (e.g., LPJ-GUESS [26, 27], O-CN [28]). Note that this categorization is somewhat arbitrary, and many features, in particular the plant-physiological core, are similar in models of different types, and some models may be referred to as intermediate types or hybrid models. As all these model types have been applied to simulate forest productivity, we here refer to all these models as “forest models,” if no distinction is warranted by the special aspects discussed in the respective text. A few key differences between these model categories are described below, where we describe the main processes in forest models. The main direct effects of eCO₂ on these processes are summarized in Fig. 2.

Photosynthesis and Transpiration

Most process-based forest models adopt a modified version of the Farquhar photosynthesis model [8] for simulating the effects of light and CO₂ on photosynthesis. The Farquhar model simulates the co-limitation of photosynthesis by carboxylation and electron transport capacities. In such models, photosynthesis increases strongly with increasing CO₂ if other resources are not limiting, as shown in Fig. 1. The specificity

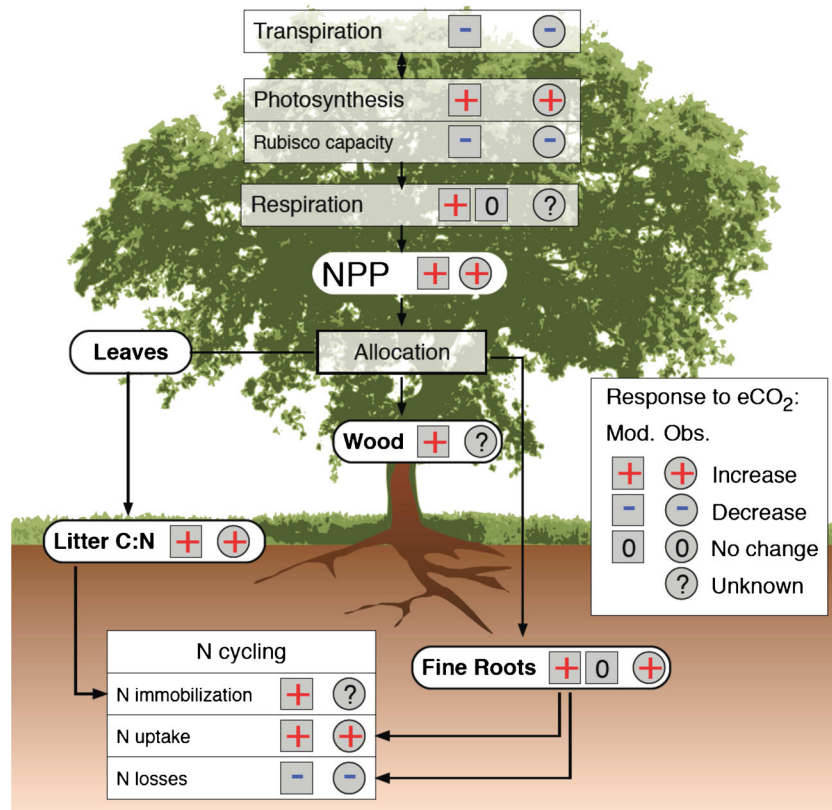


Fig. 2 Main effects of eCO₂ as simulated by common forest models that include a nitrogen cycle (squares) in comparison to findings from experiments or observations (circles). If models with different architecture simulate two clearly different responses, these two are given as separate squares. Photosynthesis and stomatal conductance are commonly closely coupled, but it is not clear whether the simulated decrease in stomatal conductance and transpiration also applies to conifers. The modelled acclimation of photosynthesis, expressed as

increasing leaf C:N and decreasing carboxylation capacity is commonly larger than observed, while the models underestimate the increase in N uptake observed in FACE experiments [29••]. Indirect effects, such as increasing transpiration as a result of increasing NPP and LAI are not captured. Nutrients other than N are not depicted because only a few models account for these. Note that this figure only depicts the most common responses. Individual models can behave differently. See text for further explanations

for CO₂ of the primary enzyme that catalyzes both the carboxylation and oxygenation (photorespiration) of the acceptor molecule of C₃ photosynthesis (ribulose biphosphate carboxylase/oxygenase [Rubisco]) decreases with temperature, implying stronger potential CO₂ fertilization at higher temperatures [2]. Acclimation to higher CO₂ occurs in the models via increased leaf C:N ratios (and associated carboxylation capacity) [29••], which also has been observed in experiments (e.g., [30]), but to a lower extent than predicted by models ([29••], see also section on FACE experiments below).

Forest models generally differ in the way limitations by environmental factors or other resources are implemented. In the widely used Lund-Potsdam-Jena (LPJ) Dynamic Global Vegetation Model (DGVM) [31], for example, an empirical temperature inhibition function is used to constrain photosynthesis at low and high temperatures. Water limitation is represented as a decrease in the stomatal conductance (limiting CO₂ uptake into the leaf) when water supply cannot meet the transpirational water demand associated with optimum photosynthesis without water limitation. Water supply is

modelled as a function of root-distribution-weighted soil water content and a maximum transpiration rate [31]. This approach takes account of the close coupling between CO₂ uptake and water loss through stomata [32]. In most models, photosynthesis and transpiration are coupled and stomatal or canopy conductance decreases with eCO₂, but the details of this coupling differ between models [33]. Water use efficiency (WUE, i.e., C uptake per unit water transpired) is generally predicted to increase under eCO₂, which has also been observed in FACE experiments [33]. An increase in WUE over the last 150 years as a result of increasing CO₂ has also been inferred from tree ring analyses and isotopic data (¹³C). However, additional analyses of ring widths indicated that the increase in WUE was not translated into increased biomass growth [34–36]. Note, however, that there is only weak, if any, evidence for conifers to reduce stomatal conductance under eCO₂ [6, 37]. Forest models generally adopt generalized schemes for the coupling of photosynthesis and transpiration, which simulate reductions in stomatal conductance for broad-leaved trees and conifers. Simulated substantial

increases in runoff because of reduced transpiration under $e\text{CO}_2$ (e.g., [38]) might, therefore, not be realistic for the large areas covered by boreal conifers [37].

Autotrophic Respiration

Part of the assimilated C is then used by respiratory processes, and the remainder is the net primary productivity (NPP), which is available for plant growth, the replacement of tissues, e.g., replacing leaf fall and fine root turnover, root exudates (not explicitly represented in most models), etc. Plant respiration is either modelled as a fixed fraction of gross primary productivity (GPP, approximately 50 %) or split into leaf respiration (scaled to maximum carboxylation capacity), growth respiration (commonly 25 % of GPP or new growth), and temperature- and tissue C:N-dependent maintenance respiration of wood and fine roots (e.g., [31]).

In the latter approach, maintenance respiration increases with temperature either adopting a Q_{10} relationship (where respiration rates increase with a fixed relative rate per given temperature increase, resulting in an exponential increase) or an Arrhenius-type response, which assumes that the Q_{10} factor decreases with temperature [39]. Models that only increase photosynthesis and simulate plant maintenance respiration independently of photosynthesis can simulate higher CO_2 fertilization (in terms of NPP) than models that scale total autotrophic respiration to photosynthesis. However, under strong temperature increases, models that assume a fixed fraction of plant respiration avoid carbon starvation that can potentially arise from increasing respiration when photosynthesis is, e.g., strongly limited by water. They can, therefore, also yield more positive NPP enhancement under $e\text{CO}_2$. If and how $e\text{CO}_2$ affects plants respiratory processes is poorly understood [40].

Allocation

NPP is allocated to different compartments of the tree, such as fine roots, stems, and leaves, and to replace tissue that is turned over (especially fine roots and leaves). This allocation is crucial for plant growth. In many models, NPP allocation is simulated by allocating a fixed fraction of assimilated C to each plant compartment. The limitation of this approach is that allocation is not responding to environmental changes such as increasing atmospheric CO_2 concentrations (e.g., [41]). Thus, a given NPP enhancement directly leads to a certain increase in biomass production. Instead, there is good empirical evidence that carbon allocation patterns can change strongly under $e\text{CO}_2$ conditions [42•]. Results from FACE experiments have shown that, under $e\text{CO}_2$, more C is allocated below ground, including fine roots, and most probably also root exudates and C transfer to mycorrhiza fungi, which can increase the N uptake by plants ([42•, 43], see also section on

FACE below). Most models do not explicitly represent root exudates and C transfer to mycorrhiza. In models that simulate increased allocation to fine roots, if nutrients become more limiting under $e\text{CO}_2$, this allocation shift also increases the nutrient uptake capacity [42•].

Nutrient Limitations

Early theoretical modelling work demonstrated that the NPP response to increasing atmospheric CO_2 should become progressively limited by N over time, a concept known as progressive nitrogen limitation (PNL). In a simple ecosystem model (the Generic Decomposition and Yield [GDAY] model), PNL occurred after a step increase of atmospheric CO_2 as N was sequestered in woody biomass and soil organic matter, leaving less soil N to be mineralized, and leaf C:N ratios increased at $e\text{CO}_2$ [44]. In this study, soil C–N cycling was simulated based on the CENTURY model [45], which has since been adopted by many forest models (e.g., LPJ-GUESS [46] and O–CN [28]). These results are consistent with experimental evidence that NPP is strongly limited by N availability in many ecosystems across the world [47], in particular in boreal forests [48].

In the widely adopted CENTURY approach, the soil N cycle is basically attached to a soil C cycle via C:N ratios of different soil organic matter and microbial pools, which can change within given bounds [45]. Thus, additional C input under $e\text{CO}_2$ locks up N if soil organic matter and/or microbial C:N ratios do not increase. It follows that carbon storage in N-limited regions can only increase if one of the following occurs: (i) total N increases, (ii) C:N ratios of a given pool increase, (iii) pools with wide C:N ratios (such as wood) increase relative to pools with narrow C:N ratios, or (iv) N losses decrease (see also [49]).

In tropical regions, P is assumed to be a main limiting factor for forest productivity (e.g., [50–53]). As in the case of N, theoretical consideration and modelling studies suggest that higher C uptake under $e\text{CO}_2$ leads to more immobilization of P in organic matter (assuming that soil organic matter C:P ratios do not substantially change), leaving less P available for plants (e.g., [12]). However, results from modelling studies also show that, under $e\text{CO}_2$, plants may actively make additional P available by increasing carbon allocation to fine roots, mycorrhiza fungi, and soil microbes and thus maintain increased productivity [51, 53], and increasing $e\text{CO}_2$ can also lead to reduced nutrient losses from the ecosystem [12]. However, we are not aware of any forest stand-scale experimental data to test these results. On the other hand, limitations from other resources, e.g., calcium or potassium, may become more limiting under $e\text{CO}_2$ (e.g., [53]) and are rarely considered in forest models. Goll et al. [54] included a simple N and P cycle in the land surface model JSBACH and found a reduced land

C uptake by 25 % compared to simulations without nutrient cycling.

In spite of the clear importance of nutrient limitations, to date, they have been ignored in many forest or dynamic global vegetation modelling studies. Not surprisingly, the model results suggested strongly increasing NPP in a future world with higher atmospheric CO₂, at least in those areas where other resources were not strongly limiting (e.g., [55, 56]). The models commonly simulated a rather “green world” in the future (e.g., [56, 57•]), which has been criticized as overly optimistic, for example, because it would be unrealistic to expect the stoichiometric N demand for the simulated increase in biomass to be met [58]. Progress has been hampered by the fact that most DGVM studies focused on the overall carbon cycle, i.e., the C sink or source strength of the global terrestrial biosphere, instead of further investigating the component processes. The results from the first global modelling studies that included N feedbacks on C cycling indeed suggested that the future C uptake by terrestrial ecosystems will be much smaller than indicated by the results of C-only models [59–62].

However, as the N cycle became incorporated into more models, it became clear that the story might not be that simple. Wårlind et al. [63•] summarized the results from a number of DGVMs run as C-only or C–N models in terms of the simulated C sequestration between the years 1850 and 2100 (using a climate and CO₂ change scenario for the future). All models except LPJ-GUESS simulated lower increases (over time) in C sequestration in the C–N version than in the C-only version (8 to 27 % lower), whereas LPJ-GUESS simulated 17 % higher C sequestration in the C–N version (even though biomass pools were generally much lower in the C–N version, in particular in boreal forests, where the simulation results appeared to be more realistic than with the C-only version). CO₂ fertilization effects were indeed substantially smaller in the C–N version than in the C-only version, but higher temperatures lead to higher N mineralization, especially in the mid to high latitudes. This climatically driven “N fertilization” led to strong increases in woody biomass growth under climate warming, which overrode soil C losses as a result of warming [63•]. Note also that additional N demand (to sustain increased biomass) under a business-as-usual climate and CO₂ scenario in the LPJ-GUESS C–N version was between the low and high N supply estimate by Hungate et al. [58] and, thus, fully consistent with their analysis [46]. The lower additional N demand in LPJ-GUESS compared to earlier DGVMs (also with the C-only version) might be rooted in the more detailed and presumably more realistic treatment of vegetation dynamics in this tree-individual-based model. Detailed representations of vegetation dynamics can result in longer lag times in the vegetation response and more realistic representations of ecosystem-scale changes in allometry (and associated C:N ratios), which emerge from the growth of individual trees. In LPJ-GUESS, additional carbon storage in mid to high

latitudes under eCO₂ and climate change were partly driven by increasing woody biomass with wide C:N ratios [46, 63•].

C Sink Limitation

As outlined above, allocation of NPP to different plant compartments and plant growth is in most forest models treated in a rather simplistic manner and strongly driven by photosynthesis. This may result from the fact that our current understanding of allocation processes is limited and that few data are available to calibrate or test models [42•]. Most forest models assume that plant growth is primarily limited by the availability of carbon (“carbon limitation”) rather than by the potential to use the available carbon (“sink limitation,” [16, 64, 65]). Sink activity may be limited under environmental conditions that are not beneficial to growth, such as low temperatures, which limit any metabolic activity, drought (e.g., as growth may also be limited by cell turgor), or low nutrient availability [66•]. These processes are not explicitly represented in most forest models. In this context, non-structural carbohydrates (NSCs) are assumed to play an important regulating role in plant metabolism (e.g., [64, 67, 68]). Such mobile NSC stores in the plant can be seen as indicators for the plants’ status regarding sink limitation [16]. Elevated atmospheric CO₂ concentrations will clearly lead to increased source activity (i.e., photosynthesis) and increased C supply but different constraints will work on the sink activity such as temperature and water limitations for tissue formation [69]. Fatichi et al. [66•] suggested that current DGVMs should be improved by treating the amount of C allocated to growth independently from NPP. Leuzinger et al. [70] developed a first attempt for simulating sink limitation to plant growth along tree lines as a result of cold growing seasons, which resulted in lower and more realistic biomass estimates by LPJ-DGVM. However, in the closely related LPJ-GUESS model, biomass at the tree line also decreases substantially when nitrogen limitation is accounted for [46], and one should keep in mind that forest models, even without explicit representation of sink limitations, include factors to account for it implicitly, such as the empirically calibrated temperature inhibition function for photosynthesis (which also constrains plant growth), or the coupling between water demand and supply in the LPJ family of models mentioned above. Nevertheless, we agree with the general criticism that current forest models are too much source-driven and that sink limitation should be addressed more explicitly in forest models.

Population Dynamics

Dynamic vegetation models, in particular, also simulate the establishment of tree saplings and tree mortality, which influence the vegetation structure and, via changes in leaf area index (LAI), forest productivity. Establishment of saplings

commonly decreases with canopy closure, and tree mortality increases as the growth efficiency, expressed as, e.g., NPP per leaf area, decreases and as trees approach their maximum age or size. These processes are strongly affected by competition for resources. As trees can reach their maximum age faster under eCO₂, increases in CO₂ could lead to higher mortality. Bugmann and Bigler [71••] used observations on the relationship between growth and longevity and the ForClim model to investigate the potential effects of feedbacks from changes in mortality on stand-level CO₂ fertilization. (Note that CO₂ fertilization effects in that study were implemented as a simple multiplier on tree growth, not mechanistically). The authors concluded that the reduction of tree longevity as a result of eCO₂ tends to offset growth-related biomass increases in the model. Even if the growth-induced reduction in longevity was not accounted for in the model, eCO₂ only led to very minor biomass increments at the stand level because of more intense competition and increases in tree mortality. These results confirm the idea that eCO₂, at least in forests with dense canopies and intense competition, only accelerates C turnover in ecosystems and has no pronounced effects on carbon storage [13]. Disturbances, such as forest pests, wind, and fire, are also important drivers of population dynamics. Forest models adopt a wide variety of approaches to represent disturbances, but summarizing these would be beyond the scope of this article.

Simulation Results Concerning CO₂ Effects on Forest Productivity

We start with summarizing model results because research on the physiological effects of CO₂ on forest productivity has been very much driven by model results. Early on, it has become clear that CO₂ effects in the models are very substantial, and that it is hardly possible to project forest productivity and carbon storage into the future without understanding physiological CO₂ effects (e.g., [55]). Then, the modelling results were increasingly confronted with data.

One common approach to capture the uncertainty associated with potential physiological CO₂ effects is to run the models with and without CO₂ effects (the latter by keeping CO₂ constant, thereby switching off both the effects on photosynthesis and stomatal conductance, but maintaining the climatic effects of CO₂). Cramer et al. [55] found that even the sign of the CO₂ transfer between the atmosphere and terrestrial biosphere projected by six DGVMs strongly depended on CO₂ effects.

The potentially crucial role of eCO₂ on vegetation productivity, biomass stocks, and the global carbon cycle has since been confirmed by many modelling studies. Ollinger et al. [72], for example, used the PnET-CN model to simulate forest growth in the northeastern USA for the period of 1700–2000.

They found substantial enhancements by increasing CO₂, although N deposition, ozone exposure, and former land use were also found to be important drivers. Also based on results from the PnET-CN model, Pan et al. [73] concluded that changes in atmospheric chemistry (N deposition, ozone, and CO₂) might have caused an NPP increase of 29 % in Mid-Atlantic temperate forests in North America during the twentieth century, of which 14 % was caused by increasing CO₂ according to the model.

Over the last decades, there have indeed been many reports of increasing forest productivity from many forest regions across the world (e.g., [74–77]). It is often assumed that CO₂ fertilization is one important driver of these increases, but this assumption is mainly based on model results (e.g., [74]). However, any increase in forest productivity over the last decades is consistent with results from forest models that respond very positively to steadily increasing CO₂ without necessarily proving causality. Successional changes, for example, could also play an important role, and the actual stand age and structure have commonly not been implemented in the models. Thus, we think that the common assumption that CO₂ effects played an important role for these increases (e.g., [78]) is not based on very solid evidence.

Regarding future projections, Pan et al. [79] used three biogeochemistry models (the Terrestrial Ecosystem Model [TEM], the BioGeochemical Cycles [BIOME-BGC] model, and CENTURY) to simulate the potential NPP response for the conterminous USA to a doubling in atmospheric CO₂. The models simulated increases between 5 and 11 %. Kirschbaum et al. [80] projected wood productivity responses of radiata pine (*Pinus radiata*) forests in New Zealand into the future using the CenW model with climate change projections from several global climate models (GCMs) and CO₂ emission scenarios from the Special Report on Emissions Scenarios (SRES). With physiological CO₂ effects enabled, the model projected an average increase of 37 % by 2090, while projected growth responses were only minor when keeping CO₂ constant. Keenan et al. [24] used the GOTILWA+ model to project the productivity of three common tree species in Spain into the future, using scenarios of climate and CO₂ change. When only including climatic effects, the model predicted average future decreases in NPP of about 30 % by the end of the century. Simulations with climatic and CO₂ effects combined gave increases of about 20 % for two species and only minor changes for the third species. Scheiter and Higgins [81], Higgins and Scheiter [82], and Scheiter et al. [83] simulated substantial future increases in forest productivity and biomass, as well as savannah to forest transitions, with the adaptive DGVM (aDGVM) across Africa and savannah regions in northern Australia. For Australia, the authors also conducted factorial experiments to separate the effects of increasing CO₂ and climate change. Under the SRES A1B emission scenario, average above-ground biomass increased from 14.2 to 32.8 t ha⁻¹ (assuming no change in rainfall seasonality). The factorial analyses revealed that only CO₂ had a

statistically significant effect on the biomass increase [83]. These simulations also highlighted the role of complex interactions between resource competition (in particular between C_3 and C_4 plants), tree population dynamics, and fire, such as a higher chance for tree saplings to escape the fire horizon under eCO_2 [81, 83].

The Amazon Forest

The future fate of the Amazon forest has received particular attention in the scientific discussion and the media since model projections indicated that large parts of the Amazon might die off by the mid-twenty-first century [84, 85]. The die-back was first simulated in the Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID) DGVM fully coupled to the HadCM3 atmosphere model. There was die-back in the model despite very strong positive CO_2 effects in TRIFFID [57••, 84] because the climate was projected to become much drier in the future. In the coupled model, the drying was also slightly enhanced by decreasing stomatal conductance that lead to reduced transpiration, which in turn also reduced precipitation [85]. Note also that substantially less die-back was simulated when scaling total plant respiration to photosynthesis instead of simulating maintenance respiration independent of photosynthesis ([86], see also section “Autotrophic Respiration” above). Also, other DGVMs (LPJ, SHE, ORCHIDEE, and HYLAND) displayed reductions in tropical carbon storage when driven by climate scenario input from the HadCM3 GCM [56]. The DGVMs generally include strong positive CO_2 effects [56], which are also expected from the basic physiology of photosynthesis (see section “Photosynthesis and Transpiration” above and, e.g., [87]). However, we do not have experimental support for such strong effects at the stand level in the tropics. Additionally, all these model versions have neglected nutrient limitation, in particular for P. The LPJmL version of the LPJ-DGVM has been applied to simulate future changes in forest biomass across the Amazon region with and without physiological CO_2 effects. The analyses revealed that the differences between the simulations with and without CO_2 effects were much larger than the uncertainty associated with the different climate change scenarios, generally with much less future biomass when CO_2 effects were switched off [88•]. The magnitude of the CO_2 effects in LPJ is here illustrated with one example simulation: Simulated climate change effects were mainly negative, in some areas with half of the current NPP by the end of the century, but the simulated combined effects of climate and CO_2 change were in most areas strongly positive (Fig. 3). Note also that, in the latest generation of GCMs, the future drying in the Amazon is much less severe, and the die-back in TRIFFID does not occur anymore [57••]. But, across the tropics, very strong positive, in our opinion uncertain, CO_2 effects override negative effects of increasing

temperatures in TRIFFID ([57••] here coupled to the MOSES land surface scheme) and other DGVMs [91].

Experimental Results and Model-Data Intercomparisons

Early experiments under laboratory conditions or with open-top chambers showed strong effects of eCO_2 (commonly around 700 ppm) on photosynthesis and plant growth [92], i.e., strong increases in photosynthesis and growth under optimal nutrient supply and lower NPP enhancements with low nutrient supplies [92]. However, the relevance of such experiments to real ecosystems has been questioned [92]. Therefore, so-called free air CO_2 enrichment (FACE, [15, 93]) experiments have been established.

FACE Model-Data Intercomparisons

In an early synthesis of the results from four such FACE experiments, Norby et al. [94] concluded that CO_2 enhancement to about 550 ppm leads to an NPP enhancement of about 23 %, which was highly conserved across a broad range of productivities. Hickler et al. [87] parameterized the LPJ-GUESS vegetation model to represent the trees and stand structure at the sites referred to by Norby et al. [94] and applied the model with weather data recorded at those sites to test whether LPJ-GUESS could reproduce the observed NPP enhancement. The model indeed predicted an average response for the sites that was similar to the observations, but the results also indicated that the FACE results from temperate forests are not representative for other climate zones. In LPJ-GUESS, the simulated NPP enhancement is larger in warmer climates because Rubisco specificity for CO_2 decreases with temperature (see above). In other DGVMs, water limitation has a stronger effect on the modelled NPP enhancement, with higher enhancement under dry conditions (compare Fig. S4 in [95] and Fig. A1 in [87]). As all these models have adopted similar representations of photosynthesis, differences in the implementation of water limitations and the coupling between C uptake and transpiration are most probably the reason for this discrepancy. A FACE result synthesis by Nowak et al. ([96], Fig. 7), however, suggests that the NPP enhancement is smaller if trees are strongly water limited, possibly reflecting sink limitation (see above).

As mentioned above, NPP enhancements do not necessarily lead to increased wood production. Increased wood production has been reported for the Duke forest (a loblolly pine [*Pinus taeda*] stand in North Carolina) for more than 10 years of CO_2 enhancement, but at the Oak Ridge National Laboratory site (ORNL, a sweet gum [*Liquidambar styraciflua*] stand in Tennessee), most of the extra C has been allocated to compartments with high turnover rates, in particular fine

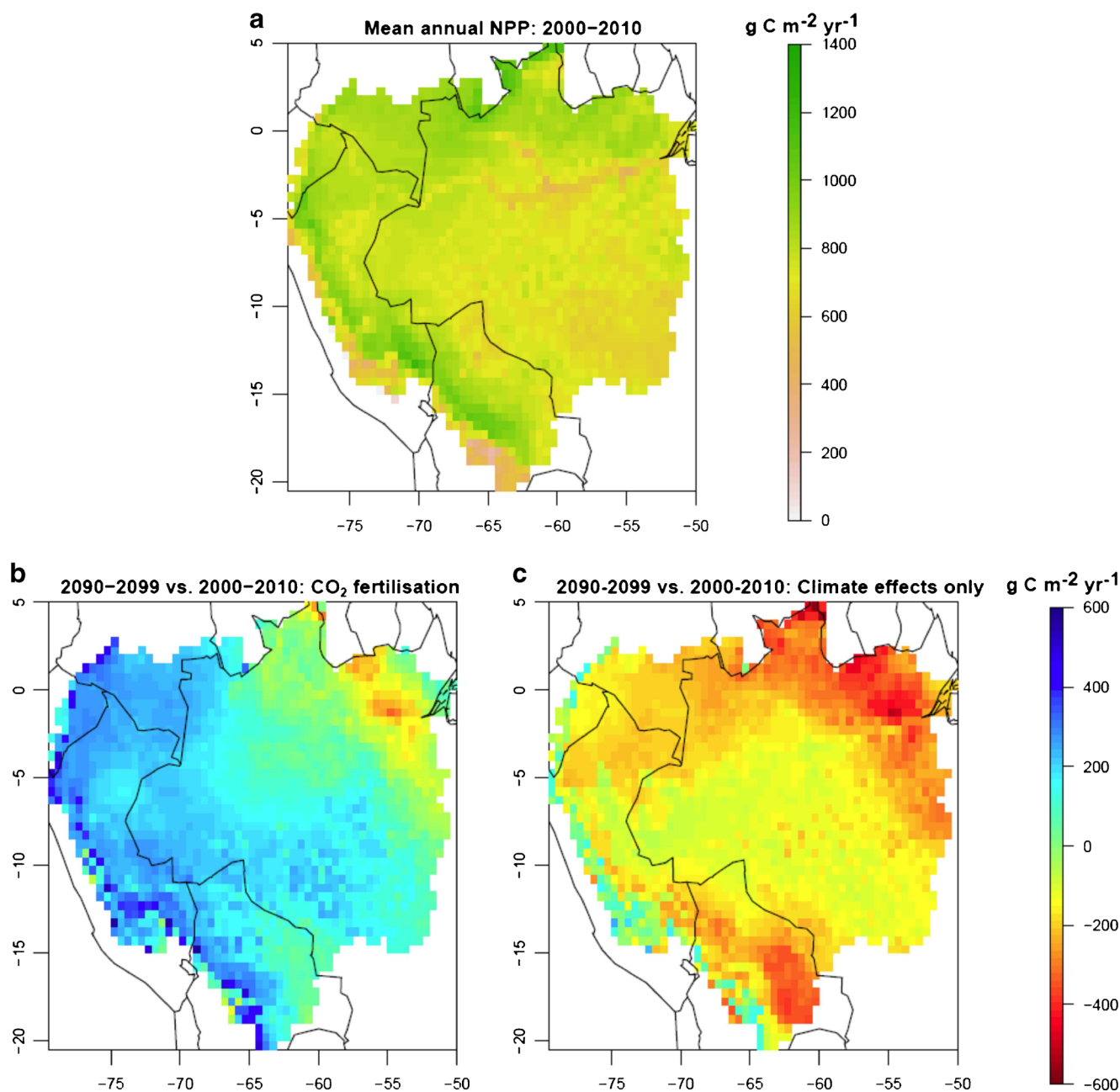


Fig. 3 Modelled net primary production (NPP) in the Amazon basin. **a** Mean annual NPP ($\text{g C m}^{-2} \text{ year}^{-1}$) for the baseline period from 2000 to 2010 and **b, c** projected changes (2090–2099 minus baseline period) with **b** CO_2 effect switched on, i.e., climate and CO_2 effects, and **c** off. Simulations for potential natural vegetation from LPJ-DGVM ([31] with updates for soil processes and hydrology [89]) forced by

HadGEM-ES climatology for RCP 8.5 provided from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 5 [90]. Modelling protocol as in [88] with an updated methodology for removing present-day biases in simulated climate (unpublished)

roots [42•, 97]. In addition, results from Duke clearly show that the NPP enhancement has been larger in FACE rings with higher nutrient availability [98], and the initial strong NPP enhancement at ORNL has not been maintained due to PNL [99•].

In 2008, the FACE model-data synthesis (FACE-MDS, [100]) project was established. In this project, four ecosystem

models, five land surface models (which are also embedded in climate models), and two dynamic vegetation models were compared to experimental results from the two of the FACE experiments that most closely resemble forests (Duke and ORNL) using a novel *assumption-centred* model inter-comparison approach, in which individual component processes of the models were compared to experimental

data [100••]. With this approach, it is possible to evaluate if individual processes in the models correspond well with experimental results and to identify shortcomings in the current models that should be addressed by further model development.

The main findings from FACE-MDS [101••] include that (i) even under nutrient-poor conditions, NPP can be enhanced under eCO₂ [29••]; (ii) simulated NPP enhancements correspond reasonably well with the experimental results, but often for the wrong reasons ([29••]; see the next two points); (iii) in the models, substantial decreases in foliar N concentration make persistent NPP enhancements possible, but the models strongly overestimate the extent of changes in C:N ratios [29••]; (iv) the models do not reproduce the magnitude of observed increases of plant N uptake under eCO₂, which, in reality, is probably caused by increased allocation of carbon below ground (fine roots, root exudates and transfer of C to mycorrhiza) [29••, 42••, 43]; (v) the results from models that use allometric relationships that vary in response to changing resource supplies correspond better with the observations than models with fixed allometric coefficients [42••]; (vi) PNL can be relaxed in models in the longer term if plant N uptake is not only a function of N supply but also of N demand, because in these models, eCO₂ leads to lower N losses [102], which is consistent with observations at ORNL [103]; (vii) the observations show that changes in stomatal conductance and photosynthesis are closely coupled, as it has been implemented in most models [33]; and (viii) even though both sites are situated in a similar climate and on similar soils, the observed responses at the sites differed markedly: PNL was very strong at ORNL [99•] but not generally across FACE rings at Duke [29••]; C allocation shifted strongly below ground at ORNL but not at Duke [42••]; priming of soil N release was stronger at Duke [29••]; leaf mass area, which has often been reported to increase under eCO₂ [3], increased substantially only at ORNL, and the pattern was not captured by any model. These large differences between the sites make it clear that further experiments will be necessary to derive generalizations that can be used in models to predict the future. Site and even species-specific responses have also been reported elsewhere. Dawes et al. [104], for example, reported that in a 9-year FACE experiment at the Swiss tree line, European larch (*Larix decidua*) showed increased tree ring increments but mountain pine (*Pinus mugo* ssp. *uncinata*) did not. Unfortunately, both the Duke and the ORNL sites have now been shut down. As a follow-up, model-data intercomparisons using the assumption-centred approach are now being carried out with the same set of models at four additional FACE sites located in the USA covering diverse ecosystems (scrub oak in Florida; mixed-grass prairie in Wyoming; desert shrub community in the Mojave Desert, Nevada; aspen clones in Wisconsin). To fill our knowledge gap concerning eCO₂ effects in the

tropics, a FACE experiment has recently been set up in a mature almost-original *Eucalyptus* forest close to Sydney (<http://www.uws.edu.au/hie/facilities/EucFACE>) and one is currently being established in the Amazon rainforest [105].

Conclusions

Understanding the physiological effects of increasing CO₂ is of utmost importance for modelling past and future forest productivity. Substantial advances have recently been made in model development, in particular concerning the coupling of N and C, and through model-data intercomparisons. Nevertheless, large uncertainties remain. These include, e.g., the response of allocation patterns under changing levels of CO₂ (in particular below-ground processes), the role of P limitation in the tropics, the functioning of C sink limitations, and feedbacks from tree population dynamics on stand-scale productivity. Increasing levels of CO₂ strongly increase photosynthesis and, in most cases, also benefit tree growth through reduced water losses. But the extent to which forest productivity in terms of wood production has and will increase as a result of eCO₂ is still highly uncertain. It seems likely that in most model simulations to date, CO₂ effects on forest wood production have been overestimated. Reducing the uncertainties will require the development of new theory, model algorithms, and rigorous comparisons between models and data. Various types of data, ranging from physiological variables, such as NSC, to results from FACE experiments and forest inventories to isotopically inferred estimates of WUE will be necessary to improve our models.

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Compliance with Ethics Guidelines

Conflict of Interest Dr. Hickler reports grants from US NCEAS during the conduct of the study.

Dr. Rammig and Dr. Werner both declare no conflict of interest.

Human and Animal Rights and Informed Consent This article contains no studies with human or animal subjects performed by the author.

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