Received: 14 June 2022 | Accepted: 29 June 2022
DOI: 10.1111/gcb.16377

PERSPECTIVE

Global Change Biology WILEY

Estimates of soil nutrient limitation on the CO_2 fertilization effect for tropical vegetation

Multiple lines of evidence support the hypothesis that the contemporary land carbon sink is primarily driven by carbon dioxide (CO_2) fertilization of vegetation growth (Walker et al., 2021). Intact tropical vegetation contribute about ¼ to this terrestrial carbon sink, but their growth appears to level-off in recent decades and their carbon sink strength declines (Hubau et al., 2020). Earth System Models (from the Coupled Model Intercomparison Projects Phase 6 [CMIP6]), however, project an increase in the strength of the tropical vegetation sink for the coming decades, since elevated CO_2 (eCO_2)-induced vegetation growth continues to outweigh climate-induced vegetation losses in their simulations (Koch et al., 2021). This mismatch between forest inventories and model projections could be the result of an incomplete representation of the limiting factors of vegetation growth to eCO_2 in models, such as the low soil nutrient availability in tropical forests. Tropical forests are predominantly late-succession forests, and found on highly weathered, nutrient impoverished soils (Quesada et al., 2012), so that their vegetation responses to eCO_2 may be strongly constrained by nutrient availability. CO_2 experiments in other climate zones indicate that nutrients strongly regulate the magnitude of the CO_2 fertilization effect, and further emerging evidence suggests little or no growth response in mature, late-succession forests (Walker et al., 2021). Tropical CO_2 experiments in tropical forests are limited to young plants and short durations, to date, but they offer empirical insights into the interaction between CO_2 and soil nutrients. Next to estimates from process-based models, these studies add direct evidence on the magnitude of soil nutrient effects on CO_2 fertilization in tropical vegetation.

We here evaluate the sensitivity of the CO_2 fertilization effect to soil nutrient availability in tropical CO_2 experiments, and compare it to the same sensitivity in an extrapolation of CO_2 effects from a synthesis of non-tropical CO_2 experiments (Terrer et al., 2019). We confront these empirical-based estimates with the sensitivity of vegetation growth to CO_2 in models from two recent model ensembles, one ensemble of terrestrial biosphere models applied for a well-monitored mature forest site in the Central Amazon (Fleischer et al., 2019) and one ensemble of the Earth System Models of CMIP6 (Arora et al., 2020). We calculate the normalized CO_2 effect on tropical vegetation carbon (vegetation β) as the percentage change in vegetation carbon, normalized to an increase of 100 ppm CO_2:

$$\left[\frac{Cveg_{elev} - Cveg_{amb}}{Cveg_{amb}} \times 100\right] \times \frac{100}{CO_{2inc}}$$

where $Cveg_{elev}$ and $Cveg_{amb}$ are vegetation carbon under elevated and ambient CO_2, respectively, and CO_{2inc} is the increase in CO_2 in ppm. We assess the change in vegetation carbon to an increase in CO_2 concentrations from approximately 370 to 600 ppm, and examine the soil nutrient feedback to eCO_2 by comparing models with and without nutrient cycles and CO_2 experiments with and without nutrient fertilization. Vegetation β is calculated for different experimental designs and time periods so that their magnitude is not directly comparable; however, we believe the effect of nutrient limitation on this common metric is informative.

The CMIP6 models derive a vegetation β of 14 ± 2% (mean ± SE, $n = 9$) for the tropical biome. The estimate is derived from the "1pctCO2-bgc" experiment, which simulates a gradual increase in atmospheric CO_2 of 1% each year, going from 372 to 616 ppm over 50 years. The change in CO_2 is not affecting the climate in this model experiment so that it discerns the pure CO_2 effect. Vegetation β was higher in the C-only models (18 ± 2%, $n = 5$) than in the nitrogen-enabled models (12 ± 1%, $n = 3$; Figure 1a). Inclusion of nitrogen cycling thus reduces the carbon-concentration feedback, that is, the land carbon uptake in response to CO_2 (Arora et al., 2020). Consideration of phosphorus cycling in Earth System Models could further reduce vegetation β in the tropics, as shown by the one model in the ensemble, ACCESS-ESM1-5, that considers coupled carbon, nitrogen and phosphorus cycles and derives a vegetation β of 5% (Figure 1a; $n = 1$).

Tropical CO_2 experiments indicate a vegetation β of 10 ± 2% ($n = 18$). Some of these experiments artificially added soil nutrients. We found vegetation β was more than three times higher in experiments with combined nutrient fertilization (16 ± 3%, $n = 7$) than in experiments without added nutrients (5 ± 2%, $n = 11$; Figure 1a). Experiments without artificial nutrient-rich soils better mimic natural conditions in tropical forests, integrating the low availability

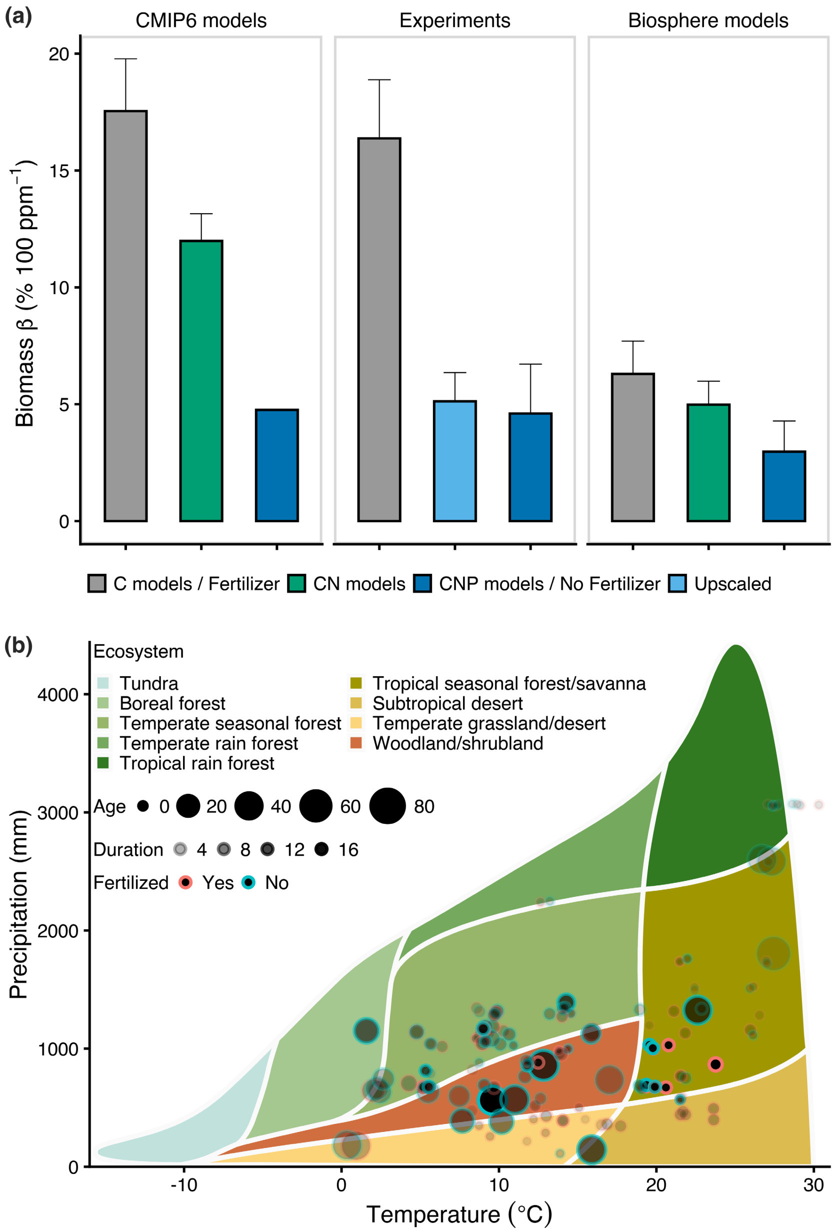

FIGURE 1 (a) Meta-data of CO_2 experiments in global climate space in terms of annual mean temperature (°C) and annual sum of precipitation (mm; adapted from Whittaker, 1975), depicting stand or plant age, experiment duration, and application of nutrient fertilizers (see Terrer et al., 2019). Tropical CO_2 experiments include open-top chambers, growth chambers, CO_2 fumigation tents, mesocosms, and glass house experiments. (b) Tropical vegetation β, defined as % change in vegetation carbon, normalized to an 100 ppm increase in CO_2 from models and experiments: The Coupled Model Intercomparison Projects Phase 6 (CMIP6) earth system models, tropical CO_2 experiments fertilized with nutrients and unfertilized, upscaling of the CO_2 experiment responses to the entire tropical biome (upscaled), and site-scale terrestrial biosphere models (see Fleischer et al., 2019). The height and error of bars indicate the mean and the standard error. Earth system model simulations from the CMIP6 model experiment "1pctCO2-bgc" were filtered for the tropical forest biome by aggregating to the forest vegetation class from the land cover map by ESA (http://maps.elie.ucl.ac.be/CCI/viewer/download.php), and the classification of tropical region is based on Pan et al. (2011), as described in Terrer et al. (2019). All models were included for which simulation results of vegetation carbon for the "1pctCO2-bgc" model experiment were available, including carbon-only models (C-models: BCC-CSM2-MR, CanESM5, CNRM-ESM2-1, GFDL-ESM4, and IPSL-CM6A-LR), models including coupled carbon and nitrogen cycles (CN models: MIROC-ES2L, UKESM1-0-LL, and CESM2), and one model including coupled carbon, nitrogen, and phosphorus cycles (CNP models: ACCESS-ESM1-5; Arora et al., 2020). The experiment "1pctCO2-bgc" increases atmospheric CO_2 annually by 1%, while all other factors remain constant. The increase in CO_2 affects only the biosphere in these simulations, and not the radiation, providing the best possible opportunity to discern the CO_2-only effect in the CMIP6 models. Simulation output of vegetation carbon was assessed for the period between the 28th year (372 ppm) and the 78th year (616 ppm). The 50-year period of atmospheric CO_2 increase was chosen to be comparable to the average CO_2 exposure and increase in the set of CO_2 experiments. Data from experiments included here are CO_2 experiments compiled in Terrer et al. (2019) classified as tropical forest ($n = 18$), which included fertilized ($n = 7$) and non-fertilized ($n = 11$) experiments. "Upscaled" data are the result of extrapolating the effect of eCO_2 as a function of nitrogen and phosphorus availabilities and nutrient-acquisition strategies from 138 eCO_2 experiments to tropical forests (see Terrer et al., 2019).

of soil phosphorus and other limiting macronutrients (Quesada et al., 2012). CO_2 experiments have predominantly been carried out in temperate experiments, with comparably few in tropical climate, and even fewer under very wet conditions (Figure 1b). Nevertheless, results from these globally distributed CO_2 experiments and their relationship with experimental site factors, including soil phosphorus, can be extrapolated to estimate the CO_2 effect across climate zones (Terrer et al., 2019). Vegetation β from this extrapolation of empirical estimates is 5 ± 2% for the tropical biome (Figure 1a).

Site-scale simulations from a terrestrial biosphere model ensemble derive a vegetation β of 4 ± 1% ($n = 14$; Figure 1a). The simulated CO_2 treatment was a step increase from 400 to 600 ppm in CO_2 concentrations over a 15-year period, mimicking the planned AmazonFACE experiment (Fleischer et al., 2019). Vegetation β was highest for the C-only models (6 ± 1%, $n = 3$), followed by models accounting for nitrogen (5 ± 1%, $n = 5$) and for combined nitrogen and phosphorus (3 ± 1%, $n = 6$; Figure 1a). Initially, higher productivity in response to eCO_2 was downregulated in the nutrient-enabled models, in particular through progressive phosphorus limitation of decomposition processes or through constraints on plant phosphorus acquisition. Models accounting for nitrogen, or nitrogen and phosphorus cycles, reproduce the constraining role of soil nutrients on vegetation β from experiments, with stronger control of combined nitrogen and phosphorus limitation in tropical forests. Assumptions on plant nutrient acquisition and plant stoichiometric plasticity in models are often barely constrained by observations, but determine their projections of soil nutrient feedbacks to vegetation growth under eCO_2 (Fleischer et al., 2019). The relatively higher vegetation β in the CMIP6 models, compared to the biosphere models, partly results from the longer simulation time, and the fact that vegetation turnover is a function of vegetation growth and carbon pool sizes in most models. Other mechanisms may potentially accelerate carbon losses but are currently not captured by models, such as CO_2-induced faster plant turnover, which would lead to reductions in vegetation β (Brienen et al., 2017).

Nitrogen and phosphorus limitation in process-based models and the omission of nutrient fertilization in CO_2 experiments thus reduces the CO_2 effect on tropical vegetation carbon notably (Figure 1a). Model estimates unconstrained by nutrients seem to present unrealistic scenarios of nutrient availability for future vegetation carbon gains, equivalent to assuming that artificial fertilizers are loaded to whole biomes. The tropical CO_2 experiments provide evidence that soil nutrients limit vegetation β but do not allow separating limitations by individual nutrients. Vegetation β from CO_2 experiments is based on experiments with short-term CO_2 exposure of young plants, most of them not exceeding a year of treatment (Figure 1b). Much slower carbon and nutrient dynamics are expected in slow-growing mature forests, and the full response of vegetation to CO_2, as well as secondary effects, may only develop over a longer time period (Quesada et al., 2012). Plants may slowly improve nutrient use and/or upregulate nutrient acquisition in response to eCO_2 with time, potentially also with associated changes in species composition. Seedlings and young plants in CO_2 experiments may also exhibit stronger responses than mature trees, due to their faster growth, and in particular in late succession forests where low vegetation growth responses are expected (Walker et al., 2021).

Our findings point to limited CO_2-induced vegetation growth in the tropics when considering soil nutrient availability. We show that the normalized CO_2 effect on tropical vegetation carbon was *c*. 70% lower in seedling CO_2 experiments without fertilizers, and *c*. 50% and 70% lower in models that consider nitrogen and phosphorus, from two model ensembles. The inadequate or lacking representation of nutrient cycles in models likely leads to overestimating CO_2 effects on tropical vegetation growth. If nutrients would limit the CO_2 fertilization effect in Earth System Models, climate-induced vegetation losses (which may also be underestimated) would be less offset and potentially turn the vegetation into a carbon source. Next to nutrient limitation on vegetation growth, the projection of a strong CO_2 fertilization effect on the tropical land carbon sink may additionally be compromised by the omission of negative feedbacks from vegetation turnover, and nonlinearity between vegetation and soil carbon accrual under eCO_2 (Terrer et al., 2021). Process-based modelers need to continue on the challenging task to incorporate our process-based understanding of carbon and nutrient dynamics in tropical forests in meaningful models, and their integration in Earth System Models. In parallel, there is an urgent need for long-term tropical CO_2 experiments in mature forests for capturing relevant processes of terrestrial carbon and nutrient feedbacks at relevant scales.

AUTHOR CONTRIBUTIONS

Katrin Fleischer and César Terrer conceived the study and wrote the manuscript together.

ACKNOWLEDGMENTS

The authors acknowledge the work of many people that were involved in conducting and analyzing CO_2 experiments, and who worked on developing models and performing model simulations that made this synthesis possible. The authors further explicitly thank Huanyuan Zhang for the extraction of CMIP6 model results, and Sönke Zaehle and Alexander Winkler for constructive comments on a previous version of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

CMIP6 model simulations are freely accessible from https://esgf-index1.ceda.ac.uk/search/cmip6-ceda/, meta-data and responses from CO_2 experiments are accessible on https://zenodo.org/record/6913071#.YuEoVC-B0Q0 (doi: https://doi.org/10.5281/zenodo.6913071), R code to synthesize data and produce the figures displayed in this paper can be accessed in https://github.com/cesarterrer/tropical-CO2.

Katrin Fleischer[1]
César Terrer[2]

[1]*Department of Biogeochemical Signals, Max-Planck-Institute for Biogeochemistry, Jena, Germany*
[2]*Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA*

Correspondence
Katrin Fleischer, Department of Biogeochemical Signals, Max-Planck-Institute for Biogeochemistry, Jena, Germany.
Email: kfleischer37@gmail.com

César Terrer, Terrer Lab, Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA
Email: cterrer@mit.edu

ORCID

Katrin Fleischer https://orcid.org/0000-0002-9093-9526

REFERENCES

Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., Schwinger, J., Bopp, L., Boucher, O., Cadule, P., Chamberlain, M. A., Christian, J. R., Delire, C., Fisher, A. R. A., Hajima, T., Ilyina, T., Joetzjer, E., Kawamiya, M., Koven, C. D., … Ziehn, T. (2020). Carbon-concentration and carbon-climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences*, *17*(16), 4173–4222. https://doi.org/10.5194/bg-17-4173-2020

Brienen, R. J. W., Gloor, M., & Ziv, G. (2017). Tree demography dominates long-term growth trends inferred from tree rings. *Global Change Biology*, *23*(2), 474–484. https://doi.org/10.1111/gcb.13410

Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., Garcia, S., Goll, D. S., Grandis, A., Jiang, M., Haverd, V., Hofhansl, F., Holm, J. A., Kruijt, B., Leung, F., Medlyn, B. E., Mercado, L. M., Norby, R. J., Pak, B., … Lapola, D. M. (2019). Amazon forest response to CO_2 fertilization dependent on plant phosphorus acquisition. *Nature Geoscience*, *12*(9), 736–741. https://doi.org/10.1038/s41561-019-0404-9

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*(7797), 80–87. https://doi.org/10.1038/s41586-020-2035-0

Koch, A., Hubau, W., & Lewis, S. L. (2021). Earth system models are not capturing present-day tropical forest carbon dynamics. *Earth's Future*, *9*(5), 1–19. https://doi.org/10.1029/2020ef001874

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, A., Arroyo, L., Chao, K. J., Dezzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., … Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, *9*(6), 2203–2246. https://doi.org/10.5194/bg-9-2203-2012

Terrer, C., Jackson, R. B., Prentice, I. C., Keenan, T. F., Kaiser, C., Vicca, S., Fisher, J. B., Reich, P. B., Stocker, B. D., Hungate, B. A., Peñuelas, J., McCallum, I., Soudzilovskaia, N. A., Cernusak, L. A., Talhelm, A. F., Van Sundert, K., Piao, S., Newton, P. C. D., Hovenden, M. J., … Franklin, O. (2019). Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. *Nature Climate Change*, *9*(9), 684–689. https://doi.org/10.1038/s41558-019-0545-2

Terrer, C., Phillips, R. P., Hungate, B. A., Rosende, J., Pett-Ridge, J., Craig, M. E., van Groenigen, K. J., Keenan, T. F., Sulman, B. N., Stocker, B. D., Reich, P. B., Pellegrini, A. F. A., Pendall, E., Zhang, H., Evans, R. D., Carrillo, Y., Fisher, J. B., van Sundert, K., Vicca, S., & Jackson, R. B. (2021). A trade-off between plant and soil carbon storage under elevated CO_2. *Nature*, *591*(7851), 599–603. https://doi.org/10.1038/s41586-021-03306-8

Walker, A. P., de Kauwe, M. G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R. F., McMahon, S. M., Medlyn, B. E., Moore, D. J. P., Norby, R. J., Zaehle, S., Anderson-Teixeira, K. J., Battipaglia, G., Brienen, R. J. W., Cabugao, K. G., Cailleret, M., Campbell, E., Canadell, J. G., Ciais, P., … Zuidema, P. A. (2021). Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO_2. *New Phytologist*, *229*(5), 2413–2445. https://doi.org/10.1111/nph.16866

Whittaker, R. H. (1975). *Communities and ecosystems*. MacMillan.