

TECHNICAL RESPONSE

CARBON CYCLE

Response to Comment on “Mycorrhizal association as a primary control of the CO₂ fertilization effect”

César Terrer,^{1*} Sara Vicca,² Bruce A. Hungate,^{3,4} Richard P. Phillips,⁵ Peter B. Reich,^{6,7} Oskar Franklin,^{8,9} Benjamin D. Stocker,¹ Joshua B. Fisher,^{10,11} I. Colin Prentice¹

Norby *et al.* center their critique on the design of the data set and the response variable used. We address these criticisms and reinforce the conclusion that plants that associate with ectomycorrhizal fungi exhibit larger biomass and growth responses to elevated CO₂ compared with plants that associate with arbuscular mycorrhizae.

In their Comment, Norby *et al.* (1) question the robustness of the conclusions in Terrer *et al.* (2). We hope that answering their queries reinforces the conclusions in the original paper:

First, Norby *et al.*'s assertion that we included entries “not relevant to the question at hand” is unfounded: Terrer *et al.* evaluated factors that influence plant biomass responses to elevated CO₂, so we used a database of experiments that measured plant biomass responses to elevated CO₂. Norby *et al.* suggest that we intentionally excluded specific experiments, but this is not so, and in fact we included as many as possible. They also recommend the exclusion of pot studies, but a priori assessment and exclusion of experiments is ill advised in meta-analysis (3). Instead, confounding factors should be postulated and tested quantitatively, as we did through mixed-effects meta-regression models, and found no evidence that growth chamber studies underestimate the CO₂ response [see figure S4 of (2)]. Regarding additional experiments that should be included in our data set, Norby *et al.* point out Flakaliden (4),

but this study was included in our original data set of aboveground biomass responses [figure S2 of (2)] and did not alter the conclusions. Nevertheless, here we conduct a validation test by excluding all pot experiments and including not one but three nonexistent (hypothetical) ectomycor-

rhizal (ECM) experiments under low N with a 0% CO₂ effect. The results of this validation test ($n = 72$) were arbuscular mycorrhizae (AM)-lowN 1.6% ($P = 0.7367$) and ECM-lowN 25.8% ($P < 0.0001$), with significant differences in AM-lowN versus ECM-lowN ($P = 0.0010$ with Bonferroni's correction). Thus, we are confident that our main finding—CO₂ stimulation of biomass under low N is greater in ECM than AM ecosystems—is robust and unbiased.

Second, we agree that productivity is a more powerful metric than biomass, in part because biomass responses are cumulative and experiments varied in duration. Relatively few data on productivity have been published from CO₂ experiments. Nonetheless, here we have performed a meta-analysis of aboveground productivity (ANPP) responses to CO₂ in N-limited studies (Fig. 1). Despite the small sample size, results support our original conclusions [figure 2 in (2)]. Norby *et al.* argue that leaf area normalization should be used to control for CO₂ effects on leaf area, but Norby *et al.*'s figure 1 represents a special case, showing a pattern that is far from universal. For example, in the Duke and Aspen free-air CO₂ enrichment (FACE) experiments, ECM trees responded positively to elevated CO₂ even when excluding all years before “canopy development was complete” (5), whereas at Oak Ridge National

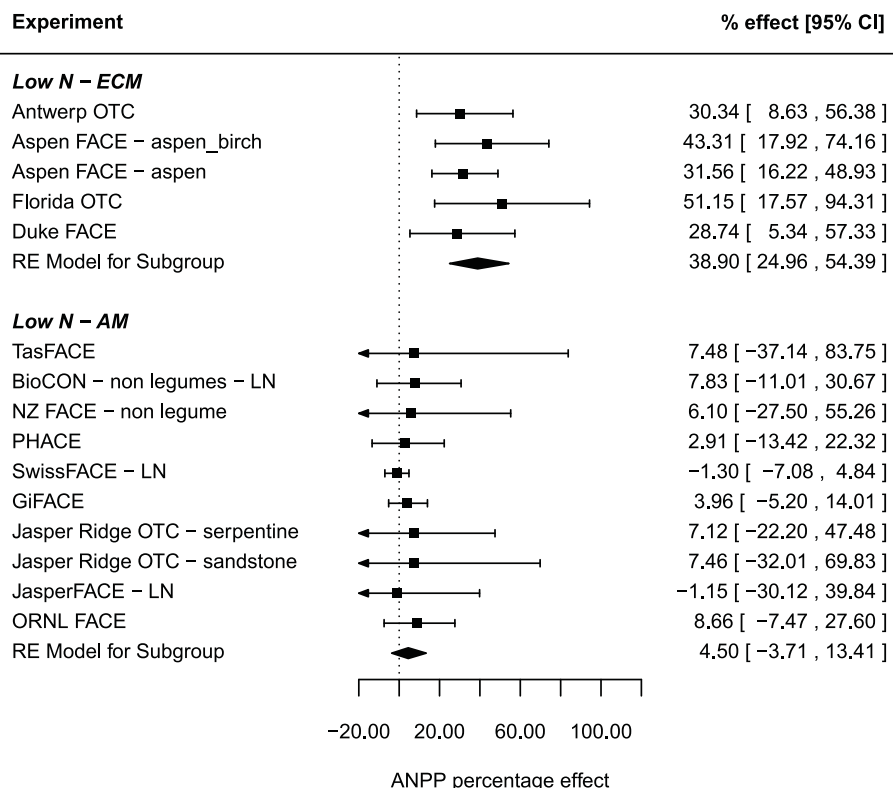


Fig. 1. Meta-analysis of CO₂ effects on aboveground net primary productivity (ANPP) for two types of mycorrhizal plants species (AM and ECM) in N-limited experiments (low N). Results for the individual studies (squares) and overall effects for the subgroups (diamonds) are given. We interpret CO₂ effects when the zero line is not crossed. Standing crop is the standard proxy for ANPP for grasslands; therefore, productivity responses in grasslands were implicitly already considered in the original paper. [References and information about the individual experiments are in table S1 of Terrer *et al.* (2).]

¹AXA Chair Programme in Biosphere and Climate Impacts, Imperial College London, Department of Life Sciences, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK.

²Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium. ³Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA.

⁴Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA. ⁵Department of Biology, Indiana University, Bloomington, IN 47405, USA.

⁶Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA. ⁷Hawkesbury Institute for the Environment, Western Sydney University, Penrith NSW 2751, Australia. ⁸Ecosystems Services and Management Program, International Institute for Applied Systems Analysis, Laxenburg, Austria. ⁹Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden. ¹⁰Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA 91109, USA. ¹¹Joint Institute for Regional Earth System Science and Engineering, University of California at Los Angeles, Los Angeles, CA 90095, USA.

*Corresponding author. Email: c.terrer@imperial.ac.uk

Laboratory (ORNL-FACE), AM trees did not (6). Furthermore, if the primary interest is in biomass accumulation, factoring out leaf area effects is inappropriate. On the contrary, because rising CO₂ and N additions affect both leaf area and growth efficiency (7), both need to be included in evaluating effects on biomass or productivity.

Third, Norby *et al.* suggested that the observed AM versus ECM response difference might simply reflect the differences between grasses and trees. When taking all studies and predictors into account, we found that plant functional type and vegetation age were not among the most important predictors [figure 1 in (2)]. Therefore, (i) the conclusions are not the result of a comparison of grasses versus trees, and (ii) there are no grounds to exclude studies with seedlings, as suggested by Norby *et al.* Nevertheless, we fully agree that more enhanced CO₂ studies in AM forests are merited.

Fourth, in contrast to ECM, AM fungi have no known saprotrophic capability to access N in complex organic forms (8). Although differences in enzyme activity among ECM fungal taxa have been reported, most ECM fungi possess the ability to synthesize enzymes that can degrade soil organic matter (9). By synthesizing available data from 10 CO₂ experiments under low N (5 ECM and 5 AM), we found that the CO₂ effect on N uptake was four times as high in ECM as in AM plants (16.30 versus 4.13%). Because N has been suggested as the most common limiting factor on growth responses to CO₂, the much larger capacity of ECM than AM plants to increase N uptake in response to elevated CO₂ likely helps explain the observed difference in growth responses to elevated CO₂.

Fifth, Norby *et al.* isolated the responses in two particular studies (in which they were involved) and invoke the progressive nitrogen limitation hypothesis, which predicts a decreasing CO₂ effect over time, to explain the observed differences. Such comparison between two sites cannot be directly compared to the outcome of

a meta-analysis with 83 sites. Clearly, various factors are at work, but as we show here and in (2), mycorrhizal type and nitrogen availability play key roles in explaining CO₂ responses across the full range of enhanced CO₂ experiments. Furthermore, we showed that the length of the treatment was not among the most important predictors [figure 1 in (2)], indicating that CO₂ responses do not generally decrease, at least over the time scale typical of experiments.

Plants typically allocate a considerable amount of C to their mycorrhizal symbionts (10), and this quantity varies with mycorrhizal type (11) and nutrient availability (12). Model developers are trying to improve representations of the N cycle (13), and there have been efforts to include better representations of roots (14), microbes, and root-microbe interactions (15). Why, then, should mycorrhizal fungi, which serve as both extensions of the root system (AM and ECM) and mineralizers of organic N (ECM), not be modeled explicitly? In fact, one of the coauthors of the critique specifically recommended including mycorrhizal associations into models (14), forming the foundation of our recommendation, which Norby *et al.* now challenge. Given emerging evidence for mycorrhizae as trait integrators (16), evidence that mycorrhizal associations may be detectable from space (17), and evidence that we have presented here and in our original analysis about the role of mycorrhizae in shaping plant responses to elevated CO₂, we maintain that there is a substantial foundation for including mycorrhizal associations in biogeochemical models. Doing so will accelerate development of the models and, over time, improve their simulations of the future biosphere.

REFERENCES AND NOTES

1. R. J. Norby *et al.*, *Science* **355**, 358 (2017).
2. C. Terrer, S. Vicca, B. A. Hungate, R. P. Phillips, I. C. Prentice, *Science* **353**, 72–74 (2016).
3. D. F. Stroup *et al.*, *JAMA* **283**, 2008–2012 (2000).
4. B. D. Sigurdsson *et al.*, *Tree Physiol.* **33**, 1192–1205 (2013).

5. R. J. Norby *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 18052–18056 (2005).
6. R. J. Norby, J. M. Warren, C. M. Iversen, B. E. Medlyn, R. E. McMurtrie, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 19368–19373 (2010).
7. R. Hyvönen *et al.*, *New Phytol.* **173**, 463–480 (2007).
8. S. E. Smith, D. J. Read, *Mycorrhizal Symbiosis* (Academic Press, Cambridge, UK, 2008).
9. J. M. Talbot, F. Martin, A. Kohler, B. Henrissat, K. G. Peay, *Soil Biol. Biochem.* **88**, 441–456 (2015).
10. E. A. Hobbie, *Ecology* **87**, 563–569 (2006).
11. M. Shi, J. B. Fisher, E. R. Brzostek, R. P. Phillips, *Glob. Change Biol.* **22**, 1299–1314 (2016).
12. S. Vicca *et al.*, *Ecol. Lett.* **15**, 520–526 (2012).
13. J. B. Fisher, D. N. Huntzinger, C. R. Schwalm, S. Sitch, *Annu. Rev. Environ. Resour.* **39**, 91–123 (2014).
14. J. M. Warren *et al.*, *New Phytol.* **205**, 59–78 (2015).
15. B. N. Sulman, R. P. Phillips, A. C. Oishi, E. Shevliakova, S. W. Pacala, *Nat. Clim. Chang.* **4**, 1099–1102 (2014).
16. G. Lin, M. L. McCormack, C. Ma, D. Guo, *New Phytol.* **213**, 1440–1451 (2016).
17. J. B. Fisher *et al.*, *Glob. Change Biol.* **22**, 2596–2607 (2016).

ACKNOWLEDGMENTS

We thank D. Blumenthal, M. Hovenden, A. Talhelm, A. Finzi, P. Newton, N. Chiariello, C. Kammann, C. Müller, C. Field, and M. Schneider, who provided data and advice. This research is a contribution to the Imperial College initiative Grand Challenges in Ecosystems and the Environment and the AXA Chair Programme in Biosphere and Climate Impacts. C.T. was supported by an Imperial College Ph.D. studentship within this program and the International Institute for Applied System Analysis (IIASA). S.V. is a postdoctoral fellow of the Research Foundation–Flanders (FWO). C.T. and S.V. acknowledge support from Climate Change Manipulation Experiments in Terrestrial Ecosystems (ClimMani) European Cooperation in Science and Technology (COST) Action (ES1308). R.P.P. acknowledges support from NSF (Ecosystem Studies Program 1153401) and DOE (Environmental System Science Program). R.P.P. and C.T. thank the Royal Netherlands Academy of Arts and Sciences, DOE, INTERFACE, and the New Phytologist trust for funding the workshop “Climate models revisited: The biogeochemical consequences of mycorrhizal dynamics.” S.V. and O.F. acknowledge support from the European Research Council grant ERC-SyG-610028 IMBALANCE-P. Part of J.B.F.’s contribution was carried out at the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the National Aeronautics and Space Administration. B.D.S. is funded by the Swiss National Science Foundation. All authors contributed to the development of the conceptual framework and to the writing of this Response.

15 September 2016; accepted 28 November 2016
10.1126/science.aai8242

Response to Comment on "Mycorrhizal association as a primary control of the CO₂ fertilization effect"

César Terrer, Sara Vicca, Bruce A. Hungate, Richard P. Phillips, Peter B. Reich, Oskar Franklin, Benjamin D. Stocker, Joshua B. Fisher and I. Colin Prentice

Science **355** (6323), 358.
DOI: 10.1126/science.aai8242

ARTICLE TOOLS

<http://science.sciencemag.org/content/355/6323/358.3>

RELATED CONTENT

<http://science.sciencemag.org/content/sci/355/6323/358.2.full>
<http://science.sciencemag.org/content/sci/353/6294/72.full>

REFERENCES

This article cites 16 articles, 4 of which you can access for free
<http://science.sciencemag.org/content/355/6323/358.3#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)