

TECHNICAL COMMENT

CARBON CYCLE

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

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Terrer *et al.* (Reports, 1 July 2016, p. 72) used meta-analysis of carbon dioxide (CO₂) enrichment experiments as evidence of an interaction between mycorrhizal symbiosis and soil nitrogen availability. We challenge their database and biomass as the response metric and, hence, their recommendation that incorporation of mycorrhizae in models will improve predictions of terrestrial ecosystem responses to increasing atmospheric CO₂.

Terrer *et al.* (1) use a meta-analytic approach to test the hypothesis that the type of mycorrhizal symbiosis interacts with nitrogen (N) availability to control the extent to which different ecosystems respond to anthropogenic CO₂ in the atmosphere. Although we accept that the hypothesis is worth testing, we believe that their analysis and conclusions are flawed, and thus the suggestion to implement mycorrhizal type as a condition to quantify the CO₂ fertilization effect on the global carbon (C) cycle within terrestrial biosphere models is premature. We outline several areas of concern:

1) Their database of CO₂ enrichment experiments includes many entries that are not relevant to the question at hand and that compromise their analysis. Interactions between C and N cycles in ecosystems cannot be evaluated from experimental results of container-grown tree seedlings in artificial soil [e.g., “Harvard” and “Basel tropical” in figure S1 of (1)]. In these early studies, elevated CO₂ (eCO₂) often stimulated growth such that the plants became root-bound, nutrient supplies were exhausted, and plant growth declined (2). Furthermore, in many of these seedling studies, there was no evidence of mycorrhizal colonization. Additional field studies (3), however, could have been included.

2) Biomass is the incorrect metric for evaluating the response of the trees in this analysis. In the Duke and Oak Ridge National Laboratory (ORNL) free-air CO₂ enrichment (FACE) experiments, about half of the biomass was present before the start of the experiment and cannot be considered a response to eCO₂. Much more

relevant for evaluating the hypothesis would be biomass increment or net primary productivity (4), and in cases of open canopies, leaf-area normalization is warranted (Fig. 1). Trees in many of the open-top chamber experiments in the Terrer *et al.* analysis were in an exponential growth phase, which cannot be sustained in forest ecosystems as leaf area becomes constrained. The substantial difference in biomass response between ectomycorrhizal (ECM) *Quercus alba* trees and arbuscular mycorrhizal (AM) *Liriodendron tulipifera* trees growing in the same soil can be attributed to the difference in leaf area deployment of the two species in interaction with exponential growth (5). When the data are expressed as growth per unit leaf area, a metric more representative of growth in a closed-canopy forest (6), the differences in biomass response disappear (Fig. 1). Hence, in many of the tree studies in this analysis, we see no basis for ascribing differential responses to mycorrhizal type.

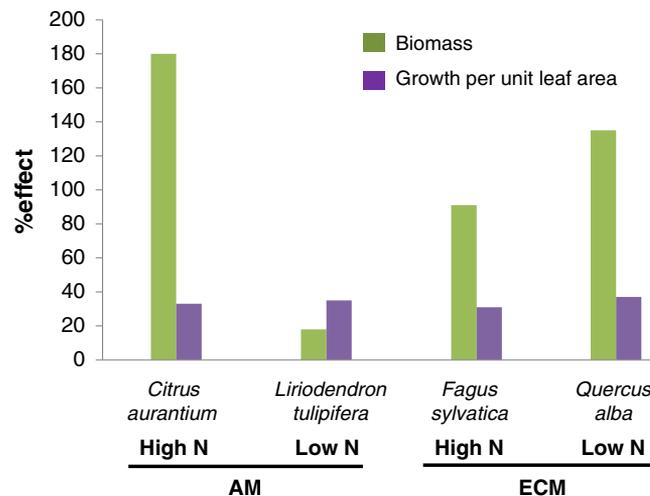


Fig. 1. Biomass response to elevated CO₂ of two AM species and two ECM species. The biomass response to elevated CO₂ of two AM species grown in field soil with open-top chambers is consistent with the pattern described by Terrer *et al.* (1)—i.e., biomass of the ECM species increased in eCO₂ in both high and low N soil, whereas the AM species responded only in high N soil. However, this pattern can be attributed to differences in leaf area development and a consequence of exponential growth, which

cannot be sustained as leaf area becomes constrained in a forest. After normalizing growth to a constant leaf area, all four species show a similar response to eCO₂. [Data source (6)] The *Citrus* and *Quercus* biomass data were used in the Terrer *et al.* analysis; the *Fagus* and *Liriodendron* data were not.

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a “starkly dichotomous” view of ECM versus AM ecosystems in terms of plant-soil feedbacks or other aspects of nutrient cycling and turnover (10). ECM likely exhibit a range of saprotrophic physiologies and therefore are not a homogeneous functional group accessing soil organic N for plant use, as conceived by Terrer *et al.*

5) The hypothesis under consideration was inspired in part by the difference in response between Duke and ORNL FACE experiments (11). The element of time is paramount in interpreting these experiments. A sustained biomass response of *Pinus taeda* (ECM) was observed at Duke, supported by increased N uptake, which was attributed to soil “priming” such that N availability increased (11). In the *L. styraciflua* (AM) stand at ORNL, an initial stimulation of biomass increment disappeared and was replaced by increased fine-root production, which supported increased N uptake, as well as increasing soil C rather than biomass C (12). Eventually, however, there was not enough available N to sustain the plant response at ORNL [i.e., progressive N limitation (13)]. The mechanism attributed to the ECM system at Duke FACE of accelerated release of organic C and N from otherwise recalcitrant pools is not a mechanism

that could be sustained indefinitely. Rather than being indicative of a fundamental difference of these two forests in responsiveness to eCO₂, mycorrhizal type, along with other differences in leaf and root turnover rates, is likely to be related more to the timing of N limitation during forest development.

Terrer *et al.* concluded their analysis with a plea to include mycorrhizal type in large-scale models so that different ecosystems could be characterized as to their potential CO₂ response. Given our concerns in how this analysis was conducted and interpreted, we think that this recommendation is missing a robust foundation.

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4. An example from an arid ecosystem experiment (not trees) in which plant biomass was the wrong metric for characterizing response comes from the Nevada FACE experiment. No differences in aboveground or belowground plant biomass were observed after 10 years of CO₂ enrichment, and these are the data used in the Terrer *et al.* analysis. But these data miss the important response of increases in net

primary productivity in wet years. The increased C input was recovered in soil pools such that net ecosystem production was significantly enhanced in this low N, AM ecosystem (14).

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ACKNOWLEDGMENTS

This research was supported by U. S. Department of Energy, Office of Science at the Oak Ridge National Laboratory. Oak Ridge National Laboratory is operated by UT-Battelle, LLC, under contract DE-AC05-00OR22725 with the U.S. Department of Energy.

12 August 2016; accepted 28 November 2016
10.1126/science.aai7976

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Science **355** (6323), 358. [doi: 10.1126/science.aai7976]

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