TECHNICAL COMMENT

CARBON CYCLE

Comment on "Mycorrhizal association as a primary control of the CO$_2$ fertilization effect"

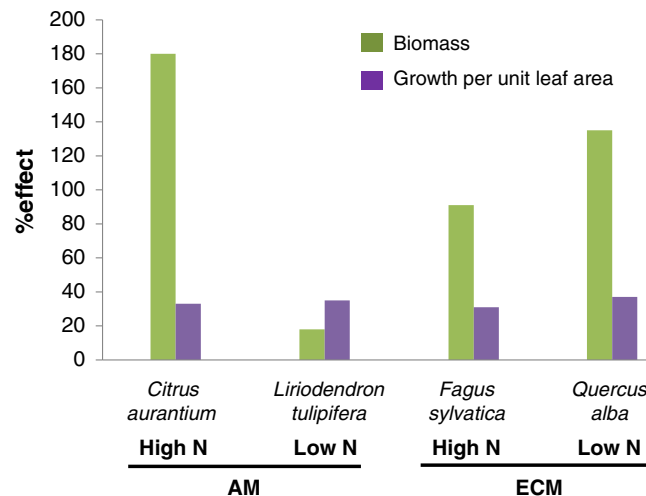R. J. Norby,[1]* M. G. De Kauwe,[2] A. P. Walker,[1] C. Werner,[3] S. Zaehle,[4] D. R. Zak[5]

Terrer *et al.* (Reports, 1 July 2016, p. 72) used meta-analysis of carbon dioxide (CO$_2$) 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 CO$_2$.

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 CO$_2$ 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 CO$_2$ fertilization effect on the global carbon (C) cycle within terrestrial biosphere models is premature. We outline several areas of concern:

1) Their database of CO$_2$ 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 CO$_2$ (eCO$_2$) 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 CO$_2$ enrichment (FACE) experiments, about half of the biomass was present before the start of the experiment and cannot be considered a response to eCO$_2$. 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.

3) Given the structure of the database used by Terrer *et al.*, the comparison of response to eCO$_2$ of AM versus ECM plants was dominated by a comparison of grasses and trees. Any mycorrhizal effects are inescapably confounded by substantial differences in morphology, growth habit, and environmental influences. If mycorrhizal type is simply a surrogate for grass versus tree, we note that differences between these plant functional types are already accounted for in models. Terrer *et al.* did run separate analyses of just trees, but there have been few studies with AM trees, and many of those in their analysis were seedling studies that probably should not have been included. The only field experiments with AM trees in their analysis [figure S1 in (*1*)] were the open-grown *Citrus aurantium* trees in high N (Fig. 1) and *Liquidambar styraciflua* trees in the ORNL FACE experiment in low N soil. This is hardly a strong basis for modeling, or even speculating about, the responses to eCO$_2$ across AM-dominated tropical forests, especially when also considering the potentially important interactions between mycorrhizae and phosphorus nutrition.

4) The purported interaction between CO$_2$, N, and mycorrhizal type is based on an assumption that ECM fungi have a capacity to access N in soil organic matter, which AM fungi cannot. Importantly, ECM fungi have independently and differentially evolved from saprotrophic ancestors nearly 80 times (*7*), and the degree to which they have retained genes with saprotrophic function differs dramatically among them (*8*). Hence, it cannot be assumed that all ECMs, especially those in undersampled regions [e.g., tropical South America, Africa, and Southeast Asia, (*9*)] have the capacity to access nutrients in soil organic matter. Furthermore, there has yet to be a definitive study demonstrating that ECM fungi actually express genes that mediate organic decay while in symbiotic association with plants. Therefore, it is incorrect to assume

[1]Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6301, USA. [2]Macquarie University, Department of Biological Sciences, North Ryde, New South Wales 2109, Australia. [3]Senckenberg Biodiversity and Climate Research Centre (BiK-F), D-60325 Frankfurt am Main, Germany. [4]Biogeochemical Integration Department, Max Planck Institute for Biogeochemistry, D-07701 Jena, Germany. [5]School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109-1041, USA.
*Corresponding author. Email: rjn@ornl.gov

Fig. 1. Biomass response to elevated CO$_2$ of two AM species and two ECM species. The biomass response to elevated CO$_2$ of two AM species and two ECM species grown in field soil within open-top chambers is consistent with the pattern described by Terrer *et al.* (*1*)—i.e., biomass of the ECM species increased in eCO$_2$ 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 eCO$_2$. [Data source (*6*)] The *Citrus* and *Quercus* biomass data were used in the Terrer *et al.* analysis; the *Fagus* and *Liriodendron* data were not.

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 eCO$_2$, 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 CO$_2$ 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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