TECHNICAL RESPONSE

CARBON CYCLE

Response to Comment on "Mycorrhizal association as a primary control of the CO_2 fertilization effect"

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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 CO_2 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 CO_2, so we used a database of experiments that measured plant biomass responses to elevated CO_2. 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 metaregression models, and found no evidence that growth chamber studies underestimate the CO_2 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) ectomycorrhizal (ECM) experiments under low N with a 0% CO_2 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—CO_2 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 CO_2 experiments. Nonetheless, here we have performed a meta-analysis of aboveground productivity (ANPP) responses to CO_2 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 CO_2 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 CO_2 enrichment (FACE) experiments, ECM trees responded positively to elevated CO_2 even when excluding all years before "canopy development was complete" (*5*), whereas at Oak Ridge National

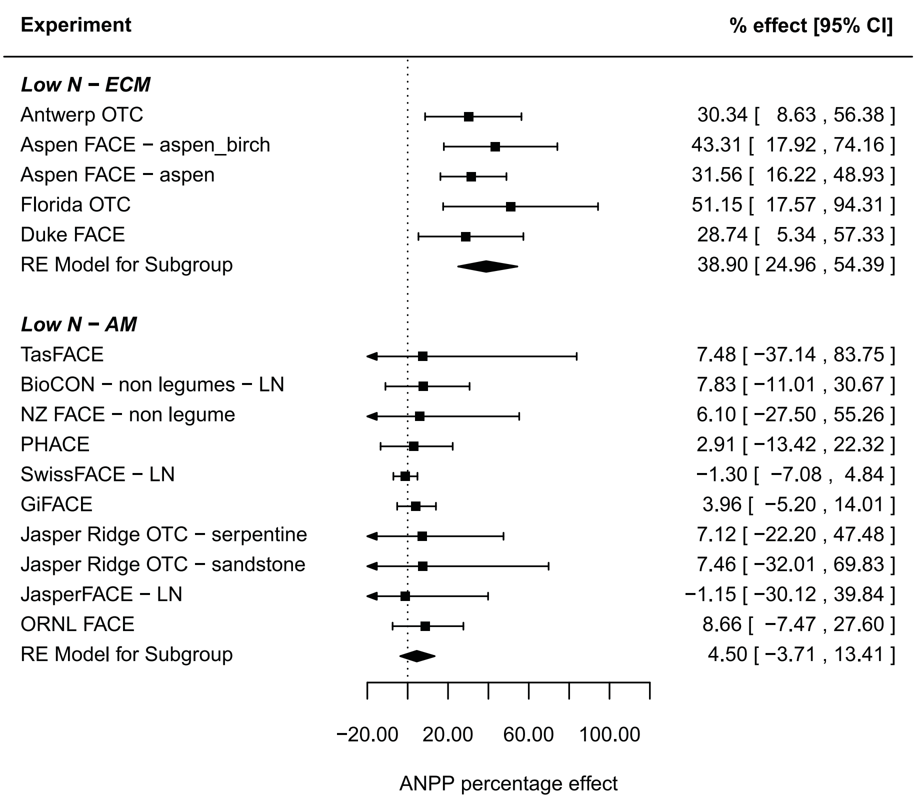

Fig. 1. Meta-analysis of CO_2 effects on aboveground net primary productivity (ANPP) for two types of mycorrhizal plants species (AM and ECM) in N-limited experiments (low N). Results for the individual studies (squares) and overall effects for the subgroups (diamonds) are given. We interpret CO_2 effects 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*).]

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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 CO_2 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 CO_2 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 CO_2 experiments under low N (5 ECM and 5 AM), we found that the CO_2 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 CO_2, the much larger capacity of ECM than AM plants to increase N uptake in response to elevated CO_2 likely helps explain the observed difference in growth responses to elevated CO_2.

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 CO_2 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 CO_2 responses across the full range of enhanced CO_2 experiments. Furthermore, we showed that the length of the treatment was not among the most important predictors [figure 1 in (*2*)], indicating that CO_2 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 CO_2, 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.

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