CARBON CYCLE

Mycorrhizal association as a primary control of the CO_2 fertilization effect

César Terrer,[1]* Sara Vicca,[2] Bruce A. Hungate,[3,4] Richard P. Phillips,[5] I. Colin Prentice[1,6]

Plants buffer increasing atmospheric carbon dioxide (CO_2) concentrations through enhanced growth, but the question whether nitrogen availability constrains the magnitude of this ecosystem service remains unresolved. Synthesizing experiments from around the world, we show that CO_2 fertilization is best explained by a simple interaction between nitrogen availability and mycorrhizal association. Plant species that associate with ectomycorrhizal fungi show a strong biomass increase (30 ± 3%, $P < 0.001$) in response to elevated CO_2 regardless of nitrogen availability, whereas low nitrogen availability limits CO_2 fertilization (0 ± 5%, $P = 0.946$) in plants that associate with arbuscular mycorrhizal fungi. The incorporation of mycorrhizae in global carbon cycle models is feasible, and crucial if we are to accurately project ecosystem responses and feedbacks to climate change.

Terrestrial ecosystems sequester annually about a quarter of anthropogenic carbon dioxide (CO_2) emissions (*1*), slowing climate change. Will this effect persist? Two contradictory hypotheses have been offered: The first is that CO_2 will continue to enhance plant growth, partially mitigating anthropogenic CO_2 emissions (*1*, *2*), whereas the second is that nitrogen (N) availability will limit the CO_2 fertilization effect (*3*, *4*), reducing future CO_2 uptake by the terrestrial biosphere (*5*–*7*). Plants experimentally exposed to elevated levels of CO_2 (eCO_2) show a range of responses in biomass—from large and persistent (*8*, *9*), to transient (*6*), to nonexistent (*10*)—leaving the question of CO_2 fertilization open. Differences might be driven by different levels of plant N availability across experiments (*11*), but N availability alone cannot explain contrasting results based on available evidence (*7*, *12*). For instance, among two of the most studied free-air CO_2 enrichment (FACE) experiments with trees, eCO_2 enhanced biomass production only during the first few years at Oak Ridge National Laboratory (ORNL)–FACE (*6*), whereas trees in the Duke University FACE experiment showed a sustained enhancement during the course of the experiment (*8*), despite N limitation. In addition to N limitation, other factors have been suggested as potential drivers of the response of plant biomass to eCO_2: age of the vegetation (*13*), water limitation (*14*), temperature (*15*), type of vegetation (*12*), or even the eCO_2 fumigation technology used (*11*). Although these factors may explain some observations, none has been found to be general, explaining the range of observations globally.

About 94% of plant species form associations with mycorrhizal fungi, an ancient mutualism thought to have facilitated the colonization of land by early plants (*16*). In this mutualism, the fungus transfers nutrients and water to the plant in exchange for carbohydrates, which are necessary for fungal growth. Mycorrhizal fungi are critical for terrestrial C cycling (*17*); are known to influence plant growth (*18*), nutrient cycling (*19*, *20*), and soil carbon storage (*21*); and respond strongly to elevated CO_2 (*22*, *23*). Yet, their impact on the N-dependence of the CO_2 fertilization effect has not been tested, despite the increasing evidence that N limitation constrains the CO_2 fertilization effect (*5*). Arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM) are by far the most widespread types of mycorrhizae (*24*): AM-plants predominate in deserts, grasslands, shrublands, and tropical forest ecosystems, whereas ECM-fungi predominate in boreal and many temperate forests (for example, those dominated by *Pinus*). ECM can transfer N to the host plant under eCO_2 to sustain CO_2 fertilization (*25*), whereas the symbiotic effects of AM fungi in N-limited systems can range from beneficial to parasitic (*19*). Hence, the association of *Liquidambar styraciflua* with AM-fungi at ORNL-FACE, and *Pinus taeda* with ECM-fungi at Duke-FACE, might explain why only trees in the latter could increase N-uptake and take advantage of eCO_2 to grow faster for a sustained period (*20*, *25*). We tested the hypothesis that the differences in the nutrient economies of ECM and AM fungi influence global patterns of the magnitude of plant biomass responses to elevated CO_2.

We synthesized data (overview is provided in table S1) on total plant biomass (grams per square meter) from 83 eCO_2 experiments (fig. S1), separating responses into aboveground biomass ($n = 83$) (fig. S2) and belowground biomass ($n = 82$) (fig. S3) in a mixed-effects meta-analysis. As potential drivers of the plant biomass response, we considered the increase in atmospheric CO_2 concentration (ΔCO_2), mean annual precipitation (MAP), mean annual temperature (MAT), age of the vegetation at the start of the experiment, vegetation type (such as grassland or forest), CO_2 fumigation technology (such as FACE or growth chamber), length of the study (years), dominant mycorrhizal type (AM or ECM), and N-status [high or low N availability, considering soil characteristics and occasional fertilizer treatments, following the approach by Vicca *et al.* (*17*) and assigning all experiments with indications for some degree of N limitation to the "low N" class and experiments that were unlikely N limited to the "high N" class] (supplementary materials, materials and methods, and table S2).

Model selection analysis, based on corrected Akaike Information Criterion (AICc), showed that the most parsimonious model within two AICc units included N-status, mycorrhizal type, and ΔCO_2 ($P < 0.001$). The relative importance of the predictors (Fig. 1) supported the removal of climate variables, length of the experiment, age of the vegetation, fumigation technology, and system type. Some predictors reduced the CO_2 effect on biomass (such as age of the vegetation), whereas others were associated with an increased CO_2 effect (such as ECM, ΔCO_2, and high N availability) (fig. S4).

The response of total biomass to an increase of CO_2 from 400 to 650 μmol mol^{-1} was larger ($P < 0.001$) in ECM (30 ± 3%, $P < 0.001$) than in AM-dominated (7 ± 4%, $P = 0.089$) ecosystems (mean ± SE, mixed effects metaregression). The overall response of total biomass was 20 ± 3% ($P < 0.001$), which is similar to previous meta-analyses (*15*), with a larger effect under high (27 ± 4%, $P < 0.001$) than low N availability (15 ± 4%, $P < 0.001$), as expected (*5*, *7*, *11*). Furthermore, we found a strong interaction between mycorrhizal type and N-status ($P < 0.001$); under low N availability, eCO_2 had no effect on total biomass of AM-dominated species (0 ± 5%, $P = 0.946$) but increased biomass by 28 ± 5% in ECM-dominated species ($P < 0.001$) (Fig. 2A). Under

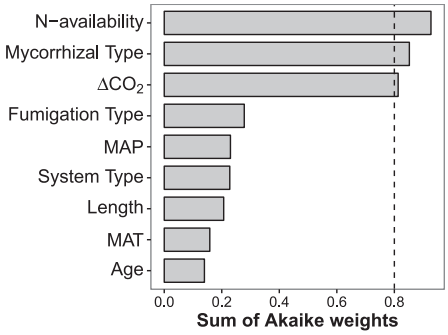

Fig. 1. Model-averaged importance of the predictors of the CO_2 fertilization effect on total biomass. The importance is based on the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples). Cutoff is set at 0.8 (dashed line) in order to differentiate among the most important predictors.

[1]AXA Chair Programme in Biosphere and Climate Impacts, Department of Life Sciences, Silwood Park Campus, Ascot, Imperial College London, UK. [2]Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium. [3]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA. [4]Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA. [5]Department of Biology, Indiana University, Bloomington, IN 47405, USA. [6]Department of Biological Sciences, Macquarie University, North Ryde, New South Wales 2109, Australia.
*Corresponding author. Email: c.terrer@imperial.ac.uk

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high N availability, the CO_2 effect on total biomass in both AM- and ECM-dominated species was significant: 20 ± 6% (P = 0.002) for AM and 33 ± 4% (P < 0.001) for ECM (Fig. 2A), with no significant differences between the two groups (P = 0.139). Hence, high N availability significantly increased the CO_2 effect in AM [post-hoc, Tukey's honestly significant difference (HSD): adj-P = 0.038] but not in ECM-associated species (adj-P = 0.999).

The patterns observed for total biomass were reflected in both aboveground and belowground biomass. Under low N availability, eCO_2 stimulated aboveground biomass significantly in ECM plants (P < 0.001), with no effect in AM plants (P = 0.584) (Fig. 2B). Similarly, eCO_2 enhanced belowground biomass in ECM plants at low N (P = 0.003) but not in AM plants (P = 0.907) (Fig. 2C).

We conducted a sensitivity analysis to ensure that the findings were robust. First, we added an intermediate level of N availability (table S2) by assigning some ecosystems that were initially classified as "low" to a "medium" class (for example, Duke, Aspen, and ORNL) (fig. S5). This enabled testing whether the large CO_2 stimulation in ECM plants was driven by experiments with intermediate N availability. Second, we weighted individual experiments by the inverse of the mixed-model variance (fig. S6) so as to ensure that the weights of the meta-analysis did not affect the outcome. Third, we ran a separate meta-analysis with the subset of experiments with trees only (fig. S7). Previous meta-analyses have reported that trees are more responsive to eCO_2 than are grasslands (*12*); as such, our findings could reflect differences of plant growth form rather than mycorrhizal association per se. Because trees are the only type of vegetation that can associate with ECM and AM (or both), an analysis of tree responses to eCO_2 can thus be used to isolate the influence of mycorrhizal type from that of vegetation growth form. These three sensitivity analyses confirmed that the CO_2 stimulation of total and aboveground plant biomass was significant and large in ECM plants regardless of N availability, whereas the effect was not significant in AM plants under low N availability. The trend was consistent for belowground biomass in ECM plants, although with high variance and low sample size, the effect was not significant (P = 0.244) under low N when the "medium" class was included.

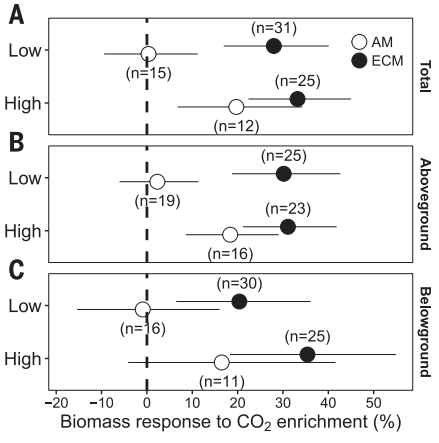

Fig. 2. Overall effects of CO_2 on plant biomass. (**A** to **C**) Effects on (A) total, (B) aboveground, and (C) belowground biomass for two types of mycorrhizal plants species (AM and ECM) in N-limited experiments (low N) or experiments that are unlikely N-limited (high N). Overall means and 95% confidence intervals are given; we interpret CO_2 effects when the zero line is not crossed.

Plant N uptake can be enhanced through mycorrhizal associations or through associations with N-fixing microbes. Some of the CO_2 experiments in our study contained N-fixing species, which might have increased N availability (table S3). eCO_2 stimulated aboveground biomass in AM species under low N by 8 ± 3% (P = 0.019) in this subgroup of experiments that included N-fixing species, whereas the remaining AM experiments under low N availability showed no biomass response to eCO_2 (1 ± 10%, P = 0.893). But even with the additional N input from N_2 fixation, the 8% biomass increase in AM plants under low N was considerably smaller than the 28 ± 5% increase found for ECM plants.

Most CO_2 experiments have been carried out in the Northern Hemisphere (fig. S8), where N, rather than phosphorus (P), is limiting. AM fungi transfer large quantities of P to the plant and hence are more likely mutualistic in P-limited ecosystems (*19*). Tropical forests are typically associated with P limitations and dominated by AM-fungi and could potentially show enhanced biomass under eCO_2. The role of nutrients on the CO_2 fertilization effect in these P-limited forests has yet to be explored (*26*).

Responses of plants to rising CO_2 are thus well explained by a simple interaction between N and microbial mutualists: When N availability is limited, only plant species that associate with ECM-fungi show an overall biomass increase due to eCO_2. Several mechanisms could explain these responses. First, ECM-associated plants typically allocate more C to support mycorrhizae than do AM plants, particularly under eCO_2 (*23*). Moreover, because ECM fungi, unlike AM fungi, produce extracellular enzymes that degrade organic N compounds (*27*), increased allocation to ECM fungi under eCO_2 may supply host plants with the N needed to sustain their growth response to eCO_2. This may explain why eCO_2 often stimulates priming effects in ECM-dominated ecosystems (*28*, *29*). Second, differences in litter quality between ECM and AM plants may influence how much N is available to be primed or decomposed. Several studies have reported that AM plants produce litters that decompose faster than those of ECM plants (*20*, *30*). Given emerging evidence that fast decomposing litters promote the formation of stable mineral-associated organic matter (*31*, *32*), much of the organic N in AM-dominated ecosystems may be inaccessible to AM plants or their associated mycorrhizae (*20*). And whereas slow-degrading ECM litters may reduce N availability in the short term, most of the N exists in particulate forms, which should be accessible to most microbes (including ECM fungi). Therefore, AM fungi are equipped with less specialized enzymes for N acquisition than are ECM and occur in soils in which N is more tightly protected. Both factors would presumably limit the enhancement of AM plant growth in response to eCO_2.

Mycorrhizal symbioses are not accounted for in most global vegetation models (*24*). Thus, the projected CO_2 fertilization effect by "carbon-only models" (*1*) is likely overestimated for AM-dominated ecosystems, which cover ~65% of the global vegetated area (*24*), albeit only when N-limited. On the other hand, global models that consider N limitation to constrain the CO_2 fertilization effect (*4*) likely underestimate responses of ECM plants to eCO_2, an area that encompasses ~35% of the vegetated area of the earth (*24*), most of which is considered N-limited by these models. Our framework reconciles the apparent discrepancy between widespread N limitation (*3*), which is assumed to limit C sequestration on land (*4*), and the observed increase over time of the terrestrial C sink (*1*, *2*), which is thought to be driven primarily by CO_2 fertilization (*33*). These results may also partly explain past findings that forests (commonly ECM) show stronger responses to eCO_2 as compared with grasslands (AM) (*12*). We propose that the CO_2 fertilization effect be quantified on the basis of mycorrhizal type and soil nitrogen status, and that large-scale ecosystem models incorporate mycorrhizal types to account for the differences in biomass enhancement by eCO_2. Mycorrhizae are ubiquitous and sort predictably with plant functional type (*24*, *34*), making feasible their inclusion in models to capture this microbial influence on global biogeochemistry. Accounting for the influence of mycorrhizae will improve representation of the CO_2 fertilization effect in vegetation models, which is critical for projecting ecosystem responses and feedbacks to climate change.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S8
Tables S1 to S4
References (*35*–*139*)

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BIRD FLIGHT

Frigate birds track atmospheric conditions over months-long transoceanic flights

Henri Weimerskirch,[1,2]* Charles Bishop,[3] Tiphaine Jeanniard-du-Dot,[4] Aurélien Prudor,[1,2] Gottfried Sachs[5]

Understanding how animals respond to atmospheric conditions across space is critical for understanding the evolution of flight strategies and long-distance migrations. We studied the three-dimensional movements and energetics of great frigate birds (*Fregata minor*) and showed that they can stay aloft for months during transoceanic flights. To do this, birds track the edge of the doldrums to take advantage of favorable winds and strong convection. Locally, they use a roller-coaster flight, relying on thermals and wind to soar within a 50- to 600-meter altitude band under cumulus clouds and then glide over kilometers at low energy costs. To deal with the local scarcity of clouds and gain longer gliding distances, birds regularly soar inside cumulus clouds to use their strong updraft, and they can reach altitudes of 4000 meters, where freezing conditions occur.

The movement of animals is driven by processes that act across multiple spatial and temporal scales. Long-distance movements such as the migrations of birds have evolved in response to large-scale environmental gradients (*1*). In particular, atmospheric conditions play a large role in determining the efficiency of migratory routes, whose consistency over years has allowed evolutionary processes to act at population levels (*2*). At smaller time and spatial scales, long-range movements have to constantly be adjusted to local conditions, in particular to minimize energy expenditure (*3*, *4*). These long movements or migrations can be done over inhospitable areas as different as deserts, high mountains, or oceans, which come with specific environmental constraints to which birds need to behaviorally and physiologically adapt their flight strategies (*5*, *6*). How these long restless flights can be energetically achieved has attracted much interest, but remains largely unknown because of the inherent difficulties of studying such behaviors in situ.

Biologists have long been attracted to locomotor extremes because they provide clear examples from which information about structure-function relationships can be drawn (*7*). Among birds, frigate birds are extreme in many aspects of their life history, including having the lowest wing loading, with a specialized capacity for soaring flight (*8*). They are also unusual seabirds because their feathers are not waterproof and their legs are small, so they are unable to land on the sea surface even though they feed exclusively at sea. They deal with these conflicting constraints by staying aloft for days when they are foraging from their nest when breeding (*9*). Probably as a consequence of these extreme attributes, frigate birds have the longest period of parental care in birds, suggesting a long period of learning to acquire flight and foraging abilities in early life (*10*). Their ability to remain airborne continuously for days is probably possible because of the capability of frigate birds to use thermals over the sea as a main energy source for soaring (*11*, *12*).

We asked how frigate birds can perform long migrations over oceans without landing and whether oceanic thermals are reliable enough in space and time to allow birds to stay airborne over long periods. To address these questions, we investigated the movement of frigate birds at several spatial scales with regard to (i) how frigate birds make use of large-scale weather systems to perform long-range movements, and (ii) how flight dynamics and energetics at a finer scale contribute to these long ranges.

We studied the three-dimensional movements and energetics of frigate birds on Europa Island (Fig. 1) between 2011 and 2015 (*13*). To study large-scale migratory movements, 24 adults and 25 juvenile birds were equipped with solar-powered Argos transmitters (*13*). To study the relationship between heart rate, activity (flapping frequency), and behavior (ascent rates and horizontal speed), 11 adult females were equipped with external custom-designed loggers measuring triaxial acceleration and electrocardiography and a Global Positioning System (GPS) device (*13*). To study movements, activity, and ambient temperature, 37 adult females and males were equipped with solar-powered GPS accelerometers, whose data were recovered regularly by an automatic recording station (*13*).

During the southwest Indian monsoon from June to October, strong trade winds occur in the southern Indian Ocean and cross the equator to form southwest winds in the northern Indian Ocean (*14*) (Fig. 1). During this season, adult frigate birds finishing the breeding season left Europa and migrated northward to take advantage of the southerly winds. They settled on roosting sites in

[1]Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France. [2]UMR 9220 ENTROPIE, Université de la Réunion, Saint Denis, La Réunion. [3]School of Biological Sciences, Bangor University, Bangor, Gwynedd, UK. [4]Department of Zoology, University of British Columbia, Vancouver, Canada. [5]Institute of Flight System Dynamics, Technische Universität München, Garching, Germany.
***Corresponding author. Email: henriw@cebc.cnrs.fr**

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Mycorrhizal association as a primary control of the CO_2 fertilization effect

César Terrer, Sara Vicca, Bruce A. Hungate, Richard P. Phillips and I. Colin Prentice

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Fungi relieve nitrogen limitation

Rising concentrations of atmospheric CO_2 stimulate plant growth; an effect that could reduce the pace of anthropogenic climate change. But plants also need nitrogen for growth. So far, experimental nitrogen addition has had equivocal effects on the magnitude of CO_2 fertilization. Terrer *et al.* explain that the impact of nitrogen on plant growth depends on the relationship between nitrogen availability and symbioses with mycorrhizal soil fungi. Only plants with ectomycorrhizal fungi associated with their roots can overcome nitrogen limitation.

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