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Review

Completing the FACE of elevated CO2 research

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Abstract

We appraise the present geographical extent and inherent knowledge limits, following two decades of research on elevated CO2 responses in plant communities, and ask whether such research has answered the key question in quantifying the limits of compensatory CO2 uptake in the major biomes. Our synthesis of all ecosystem-scale (between 10 m2 and 3000 m2 total experimental plot area) elevated CO2 (eCO2) experiments in natural ecosystems conducted worldwide since 1987 (n = 151) demonstrates that the locations of these eCO2 experiments have been spatially biased, targeting primarily the temperate ecosystems of northern America and Europe. We consider the consequences, suggesting fundamentally that this limits the capacity of the research to understand how the world’s major plant communities will respond to eCO2. Most notably, our synthesis shows that this research lacks understanding of impacts on tropical forests and boreal regions, which are potentially the most significant biomes for C sink and storage activity, respectively. Using a meta-analysis of the available data across all biomes, we show equivocal increases in net primary productivity (NPP) from eCO2 studies, suggesting that global validation is needed, especially in the most important biomes for C processing. Further, our meta-analysis identifies that few research programs have addressed eCO2 effects on below-ground C storage, such that at the global scale, no overall responses are discernable. Given the disparity highlighted in the distribution of eCO2 experiments globally, we suggest opportunities for newly-industrialized or developing nations to become involved in further research, particularly as these countries host some of the most important regions for tropical or sub-tropical forest systems. Modeling approaches that thus far have attempted to understand the biological response to eCO2 are constrained with respect to collective predictions, suggesting that further work is needed, which will link models to in situ eCO2 experiments, in order to understand how the world’s most important regions for terrestrial C uptake and storage will respond to a future eCO2 atmosphere.

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1. Introduction

Over two decades, plant and ecosystem responses to future elevated atmospheric CO2 (eCO2) levels have been examined by experimental manipulation. Such research was tasked with understanding how this
global environmental change factor will affect plants and communities and how they influence carbon budgets for the future. Predicting vegetation responses to eCO2 is important because it may directly alter future net primary productivity (NPP) in ecosystems across the globe (Korner, 2006), thereby modulating carbon dynamics and the balance of terrestrial carbon. Experimental free air CO2 enrichment (FACE) of semi-natural plant communities was implemented to determine the capacity of terrestrial ecosystems to sequester carbon under future conditions of eCO2. This research demonstrated initially higher rates of photosynthesis (Korner, 2006; Norby and Zak, 2011), stimulation of above- and below-ground biomass and increased microbial and soil C (Ainsworth and Long, 2005; Luo et al., 2006). However, plant communities often acclimate to eCO2 in the long-term and above ground growth rates do not continue to positively respond to CO2 addition (Reddy et al., 2010; Norby and Zak, 2011). Uncertainty as to the duration of the eCO2 response and its variation globally limits our ability to predict how plant communities will continue to take up additional anthropogenic CO2 in the atmosphere. In an assessment of such research presented herein, we suggest that throughout its experimental history, a collective spatial bias has existed in eCO2 research which is weighted towards temperate biomes (Korner, 2009; Luo et al., 2006, 2011). eCO2 research has therefore missed important regions with large C sink potentials, including globally significant biomes, such as boreal and tropical forest. With many eCO2 experimental programs now in decline, questions are out-

3. Integrating elevated CO2 experiments with model predictions of future C sink capacity

Over the last two decades, predictions of the terrestrial sink capacity have been made using dynamic global vegetation models (DGVMs). These models synthesize the best understanding of physiological processes and vegetation dynamics, to predict terrestrial carbon fluxes, in response to future global change factors, including eCO2. Collectively, however, such models exhibit a wide range of sensitivities to future conditions (of CO2 and climate) and exhibit asynchronous behavior under different scenarios (Sitch et al., 2008; Galbraith et al., 2010). The outcomes suggest that our present empirical understanding is insufficient, particularly in terms of soil nutrient limitation and ecosystem responses to eCO2 (Fisher et al., 2013). So far, DGVM predictions for eCO2-induced changes in NPP have only been experimentally validated via comparisons with a limited subset of eCO2 experiments in temperate forests (n = 4) (Sitch et al., 2008; Norby et al., 2005). Such forests are widely considered to be constrained by soil nitrogen (N) (Finzi et al., 2006). At a global scale such conditions are atypical, because many regions are phosphorus-limited (Lloyd et al., 2001) and also sequester carbon under very different conditions of temperature, precipitation and sunlight availability. The influence of global variations in environmental conditions appears largely untested by eCO2 research, yet historically DGVMs have only been validated on the basis of this limited number of temperate experiments. To improve our confidence in such models, a better understanding is needed to verify how component soil–plant processes respond to and interact with eCO2 at the global scale. Long-term eCO2 experiments in major global regions for C storage and sequestration are potentially the most direct way of achieving this.

4. Appraising the extent of historic eCO2 experimentation via a global biological synthesis

We conducted an appraisal of all eCO2 experiments since 1987, using the following combined search terms in an ISI Web of Science search: “elevated CO2”, “FACE”, “CO2 enrichment” and “ecosystem.” Our specific aim was to consider typical experiments relevant to natural ecosystems, so sources were excluded to remove any investigations using controlled environment chambers or enclosed greenhouses to simulate eCO2 conditions. Similarly, studies were also excluded if their primary focus was on crop species. Our final synthesis identified 675 papers from 151 unique studies (with a 10 m2 – 3000 m2 range in total experimental plot area) investigating ecosystem-level responses to eCO2 worldwide, since 1987, when the wider adoption of eCO2 methods first emerged for ecological studies. Of these experiments nearly 44% used FACE technology, whereas others utilized open-top chambers (48%), naturally-occurring CO2 springs (5%) or CO2 systems fitted to the branches of entire trees (3%). The FACE system has the least impact on other growing conditions including microclimate, but is inherently costly and may not
be suitable in some locations. By contrast, experimental artifacts introduced by open-top chambers, such as warmer and more humid conditions, and reduced air flow, can enhance plant growth responses to eCO2 (Kimball et al., 1997).

Spatial coordinates were extracted from each published study and converted to standardized World Geodetic System (WGS) global grid values for latitude and longitude. Where these data were not presented, methodological descriptions of experimental locations were used to derive equivalent WGS data. Experimental coordinates were integrated with globally modeled estimates of biological functioning for (1) living C density (Ruesch and Gibbs, 2008), (2) NPP (Imhoff and Bounoua, 2006), (3) soil C density (Matthews et al., 2000) and spatial delineations of biome extent (Olson et al., 2001), using ESRI ArcMap 9.3 (ESRI, 2008). Our synthesis of experimental analyses of soil C responses to eCO2 was obtained using a standard meta-analytical technique, by calculating the log response ratio (RR) (Curtis, 1996) for mean values of organic or total soil C content (typically within a 0–30 cm sampling depth) between the eCO2 treatment (~700 ppm) $x_1$ and ambient “control” (~360–390 ppm) $x_c$, where:

$$RR = \ln (\frac{x_1}{x_c}) = \ln (x_1) - \ln (x_c)$$

In cases where other experimental factors existed (e.g. nitrogen addition or different soil types), soil C values took the collective mean of all CO2 treatment and all ambient CO2 groups, regardless of other interacting factors. Because of a range of methodologies in soil assays for each of the studies assessed and a lack of common units, the log response ratio allowed different studies to be validly compared (Curtis, 1996). In cases where soil C data from multiple years were published from a single experiment, the latest published values were used, which were typically towards the end of experimentation. For primary productivity, we used a similar approach, taking the latest published mean experimental values for common and related metrics of above ground plant growth, including total biomass, extracted from 41 experiments. Where results for multiple species were presented in one experiment, a log response ratio was individually calculated using data from each species, and a mean value taken from the log response ratio for all species. Our analysis of experimental soil C used values for organic or total soil C content from each experiment, where available. Analyses of soil C were conducted in only 24 out of 151 total eCO2 experiments (16%).

Total CO2 emission levels per country for 2004 were obtained from the UN Millennium Development Goals Inventory database for CO2 emissions (CDIAC, 2012). These were compared with the total number of eCO2 “project years” per country, which was defined as the sum experimental duration of all individual eCO2 projects (between 1987 and 2011), according to each country.

5. Evaluating the global coverage of elevated CO2 experiments

Our synthesis shows that eCO2 experiments are highly concentrated around North American and European ecosystems (Fig. 1), which is a strikingly unbalanced arrangement when considered against globally modeled metrics for C storage and sequestration capacity, including total vegetation biomass (above- and below-ground) (Ruesch and Gibbs, 2008), net primary productivity (NPP) (Imhoff and Bounoua, 2006), or soil C capital (Matthews et al., 2000) (see Fig. 1a–c). In particular, our spatial experimental projection demonstrates how lack of eCO2 research in biomes with greatest carbon storage fundamentally constrains our ability to predict C dynamics globally. Areas with the largest terrestrial influence on C dynamics globally, most notably tropical, tundra and boreal regions (Fig. 2a) (Korner, 2006; Ainsworth and Long, 2005), have been largely ignored.

Our literature search found that the majority (59%) of all experiments investigated lasted 3 years or less and (of these ~70%) focused on above-ground responses. Some industrialized or newly-industrialized countries with large contributions to global CO2 emission rates have hitherto invested relatively little in eCO2 experimentation (Fig. 2b). In many instances these countries host forest habitats globally important for C storage and wider provision of ecosystem services, including biodiversity. An opportunity exists for these countries to become further engaged with eCO2 in order to understand how this factor will directly alter forest productivity within their borders and determine C dynamics globally. Using this knowledge, collaborative research frameworks could inform policy development by accounting for the enhanced CO2 uptake in certain forest types, while quantifying effects to other ecosystem services. For example, eCO2 can enhance fecundity in natural ecosystems (Way et al., 2010; Gwynn-Jones et al., 2012) and may interact with other global change factors, including warming and nitrogen deposition, to alter relationships with pollinators (Hoover et al., 2012). Even if CO2 productivity enhancement effects are shown to be transient, the ecological uncertainty associated with this transformation as it develops over multi-decadal time-scales means that further improvements in our understanding will be highly policy-relevant. Our review demonstrates, however, that experimental investment in eCO2 programs has scaled back globally since the turn of the millennium (falling from a “peak” of 77 papers in 2001, to 27 in 2011) (see Supplementary data S1). If, as we argue, further research is an outstanding necessity, on-going coordinated financial input will be required from both industrialized and newly-industrialized countries across the globe.

Of the 151 experiments investigated, longer-term experiments (>3 years) accounted for 42% (63 experiments) of the research, with only 17% (25 experiments) examining eCO2 effects on below-ground C storage processes. Measures of primary productivity were examined in 27% (41) of the experiments (Fig. 3a), with 6 biomes remaining unstudied, including those in most tropical and boreal regions. Experimental responses to eCO2 measured via primary productivity were most variable in the temperate forest biome, which has also hosted the greatest number of studies. Only 16% of all experiments studied (24 from 151) had specifically looked at soil C, suggesting that eCO2 effects on below-ground C dynamics are poorly understood at the global scale. Importantly, results from a limited number of whole ecosystem studies involving total experimental areas of between 10 m2 and 3000 m2 (25) have detected gains for soil C in the most studied temperate deciduous forest biome, but for all other biomes the data are too limited to discern any reliable patterns (see Fig. 3b).

6. What uncertainties come with limited elevated CO2 research on tropical ecosystems?

Tropical forest ecosystems possess the largest biologically active C stocks (de Deyn et al., 2008), which account for ~70% of the gross C uptake by the world’s forests (Pan et al., 2011). Tropical forest litter and soils are also a significant reservoir of C, accounting for ~34% of all litter and soil forest C globally. As highlighted by Hickler et al. (2008), certain functional characteristics of tropical ecosystems, combined with high rates of productivity, suggest that this biome has a capacity for stronger eCO2 responses than its temperate equivalent. Modeling and atmospheric sampling analyses support such a widespread biological response, repeatedly implicating tropical forests as the major global sink for anthropogenic C (Fishier et al., 2013; Hickler et al., 2008; Stephens et al., 2007), yet the spatial extent and characteristics that support this tropical “sink” are yet to be verified from ground-truthing surveys using limited scale measurements of tropical tree growth rates over time to investigate this (Clark et al., 2003, 2010).

Leguminous N-fixing species and evergreen broadleafed species are a large component of tropical forest biomass and also known to be especially physiologically responsive to eCO2 (Rogers et al., 2009; Niinemets et al., 2010). Furthermore, eCO2 can also lower the photosynthetic light compensation point, thereby increasing photosynthetic efficiency, particularly in the deeply shaded tropical understory (Korner, 2009). In short, a combination of ecophysiological mechanisms such as these could potentially account for increased tropical CO2 uptake, yet none
have been extensively studied under eCO2 conditions in tropical forest. Hypothetically, tropical habitats enriched with certain plant functional types (such as legumes), particular soil characteristics (e.g. differences in nutrient cycling capacity), or vegetation disturbance history (Foody et al., 1996; Pan et al., 2011), could each modulate the tropical eCO2 sink capacity, either individually or in combination. Addressing the influence of factors such as these alongside eCO2 would address a present research shortfall and identify the specific ecosystem characteristics allowing this sink to function. If such research were developed in order to define the tropical sink it would provide invaluable information and potentially demonstrate which habitat types are most important for CO2 sequestration. In this way, future conservation priorities could be targeted appropriately for these tropical systems.

7. The uncertain future of carbon in the boreal forest and tundra regions

The boreal forest and tundra biomes are also very poorly represented in terms of eCO2 research (Fig. 2a). Estimates suggest that together 540–1700 Gt of C is stored in the soils and living biomass of these biomes (UNEP-WCMC, 2008; Tarnocai et al., 2009) (see Supplementary data S1). Most C (ca. 85%) in the boreal forest biome is stored in soil (Malhi et al., 1999) and understanding the response of this immense carbon reserve to combined global changes, including eCO2, remains a research priority. It is uncertain whether increased C sequestration will occur with eCO2 conditions and under a warming atmosphere. However, we need to establish if the addition of new carbon,
particularly with warmer conditions, is likely to prime the release of old carbon from these soil stores (Freeman et al., 2004; van Groenigen et al., 2014), thereby positively feeding back on eCO2.

8. A way forward

From our synthesis we conclude that a global strategy for eCO2 research needs to be completed. Outstanding needs include accounting for remaining uncertainty in the effects of eCO2 on plant productivity and soil C storage. Such information is essential in order to effectively predict global C dynamics under a future eCO2 climate, particularly in the most understudied ecosystems with the greatest potential influence on C dynamics globally. At a global scale, these are the highly productive forests of the tropics (Pan et al., 2011) and the soils of tundra and boreal regions (Tarnocai et al., 2009), both of which have been largely overlooked by long-term eCO2 research programs. Long term eCO2 experimentation in these areas would support integrated modeling with improved resolution for these biomes, in order to integrate plant and soil processes at the global scale. To be effective, this research would need to be coordinated and follow standardized protocols for plant productivity assessments and soil C fluxes. This could be integrated with existing global carbon dynamics studies that have standardized methodologies for C dynamics monitoring, such as the Global Ecosystems Monitoring Network (GEM) which uses a network of 1 ha forest plots (Matthews et al., 2012). A network of spatially smaller eCO2 experiments could be embedded to build on existing knowledge and expertise. Such an approach would deliver a thorough account of above and below ground fluxes in both plant productivity and soil carbon in response to eCO2. By standardizing measurements and instrumentation, direct comparisons could be made between a range of forest plant communities, thereby allowing the spatial and temporal limits of the CO2 fertilization effect to be quantified according to climate, habitat type and disturbance history, within major biomes for C sink activity.

Importantly the new generation of eCO2 experiments needs to be designed to have a low carbon footprint, possibly utilizing CO2 "wastes" and local resources (e.g. CO2 springs) also having precise control systems that recirculate CO2 enriched air achieved via solar powered fans. This would respond to our environmental responsibility as researchers and at the same time make experimentation cost effective for longer term research.

Our synthesis demonstrates a spatial disparity in eCO2 research that may now open up possibilities for several newly-industrialized
countries that host ecosystems of global significance within their borders. However, it should be noted that many tropical regions of Asia and South America are also presently subject to elevated nitrogen (N) deposition rates that are projected to intensify (Dentener, 2006; Boy et al., 2008; Hietz et al., 2011). Our existing understanding of N × eCO2 interactions remains relatively limited (only 21 temperate experiments of the 151 eCO2 experiments in our analysis examined N deposition interactions). However, research in temperate forests suggests that elevated N deposition increases carbon sequestration (Thomas et al., 2009). For boreal regions where high-latitude warming is a more significant future priority, further research on interactions between warming and eCO2 is needed, because increased plant productivity could prime old carbon release from the soil via inputs of new carbon. To our knowledge only two high latitude eCO2 experiments have investigated interactions with warming, demonstrating significant eCO2 treatment effects on tree growth (Kilpeläinen et al., 2005) and mainly temperature effects on above ground growth in sub-arctic dwarf shrubs (Olsrud et al., 2010). However, the latter study highlighted the effects of CO2 on mycorrhizal colonization but did not consider root growth and belowground C.

More widely, other global climate factors, such as changing precipitation levels, may modulate eCO2 responses via influences on plant productivity and soil carbon dynamics, particularly in regions that experience dry conditions. For example, eCO2 induces the accumulation of non-structural carbohydrates in grasses and trees, particularly under drought conditions (Duan et al., 2013; AbdElgawad et al., 2014). Induction of such compounds and other physiological responses including effects on stomata can improve tree seedling drought survival (O’Brien et al., 2014). eCO2 would therefore alter the capacity of some plant communities to regenerate and withstand drought under changing climatic conditions. A new program of eCO2 research would therefore need to incorporate further relevant climate manipulations where suitable. For industrialized countries that have already undertaken eCO2 experimentation, now is the time to collaborate, to share expertise and to “think globally rather than locally.” The opportunity remains to tackle the outstanding question about eCO2 and plant-mediated carbon dynamics.
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