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Review

Completing the FACE of elevated CO₂ research



Alan G. Jones^{a,1}, John Scullion^a, Nick Ostle^b, Peter E. Levy^c, Dylan Gwynn-Jones^{a,*}

^a Institute of Biological Environmental and Rural Sciences, Aberystwyth University, Ceredigion, SY23 3DA, Wales, UK

^b Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

^c Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, Scotland, UK

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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

* Corresponding author. Tel.: +44 1970 622318; fax: +44 1970 622350.
E-mail address: dyl@aber.ac.uk (D. Gwynn-Jones).

¹ Present address: Earthwatch, Mayfield House, 256 Banbury Road, Oxford, OX2 7DE, UK.

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 outstanding regarding the effect of eCO₂ on global carbon budgets. Given a geographical bias we observe in experimental locations, we reappraise what has been learnt and consider remaining uncertainties. A disparity exists between the global distribution of eCO₂ experiments and hotspots for NPP, total plant biomass-carbon and soil-carbon. We review how such limitations might affect our capacity to predict atmospheric CO₂ uptake for the future and, thereby, constrain the effectiveness of policy decisions relating to the world's major terrestrial biomes for C uptake and storage. By indicating opportunities for future development in this area we suggest how researchers and policymakers can work together to understand the global impact of eCO₂ on plant communities and ecosystem services to complete the FACE of elevated CO₂ research.

2. Defining the “missing sink” for eCO₂

With ongoing increases in the rates of CO₂ emitted from anthropogenic sources globally (den Elzen et al., 2013), a pressing need remains to quantify the consequences of elevated atmospheric CO₂ (eCO₂), not only for our climate, but also to account for its impact to the global spread of plant systems sequestering CO₂ via photosynthesis. Elevated CO₂ has been considered a possible future driver of increased productivity in some plant systems globally via a “CO₂ fertilization” effect (Fisher et al., 2013). This effect provides a mechanism whereby some climatic impacts of increasing atmospheric CO₂ may be buffered by plants and ecosystems. Possible evidence for a large-scale fertilization and sequestration effect comes from the striking mismatch between the rate of increase of anthropogenic CO₂ emissions and slower observed changes in atmospheric concentrations, suggesting that a terrestrial “carbon sink” may be buffering CO₂ increases and limiting global warming (Field, 2001). Despite the importance of this phenomenon, this sink has been poorly characterized by either experimental or modeling approaches (Norby and Zak, 2011). Hence, the specific ecosystems and ecophysiological interactions responsible are largely uncertain. Identifying the underlying mechanisms remains an international, yet elusive, research priority, particularly as the capacity for such a sink to continue to sequester additional C is unknown (Luo et al., 2006; Luyssaert et al., 2007).

The limits of terrestrial ecosystem CO₂ sequestration are determined by the C dynamics of individual plant communities, particularly, rates of net primary productivity (NPP) and below-ground C transfer integrating with soil characteristics. In turn, plant productivity may be constrained by nutrient dynamics and various abiotic factors that limit growth.

These include variations in soil macro-nutrients such as nitrogen (N) and phosphorous (P) (Reich et al., 2006; Langley and Megonigal, 2010), which differ in soil availability considerably at the global scale. Considerable uncertainties exist, therefore, in quantifying the limits of ongoing eCO₂ uptake via long-term increases in plant productivity from CO₂ fertilization (Karnosky, 2003). The most direct basis on which to predict such responses, however, is through eCO₂ experimentation (Korner, 2006). This approach also allows key factors (such as soil nutrient characteristics) to be considered, either by exploiting differences due to spatial variability, or by direct manipulation of such factors under experimental conditions. Experimental manipulation also allows research questions to be targeted at the most appropriate ecosystems. However, field experimentation examining eCO₂ effects on ecosystems has declined significantly owing to funding reductions in this area of ecology, potentially leaving important gaps in our understanding of terrestrial C dynamics and how these relate to an eCO₂ future.

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 plant-soil 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) \bar{x}_t and ambient “control” (~360–390 ppm) \bar{x}_c , where:

$$RR = \ln(\bar{x}_t/\bar{x}_c) = \ln(\bar{x}_t) - \ln(\bar{x}_c)$$

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 (Fisher 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 broadleaved 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

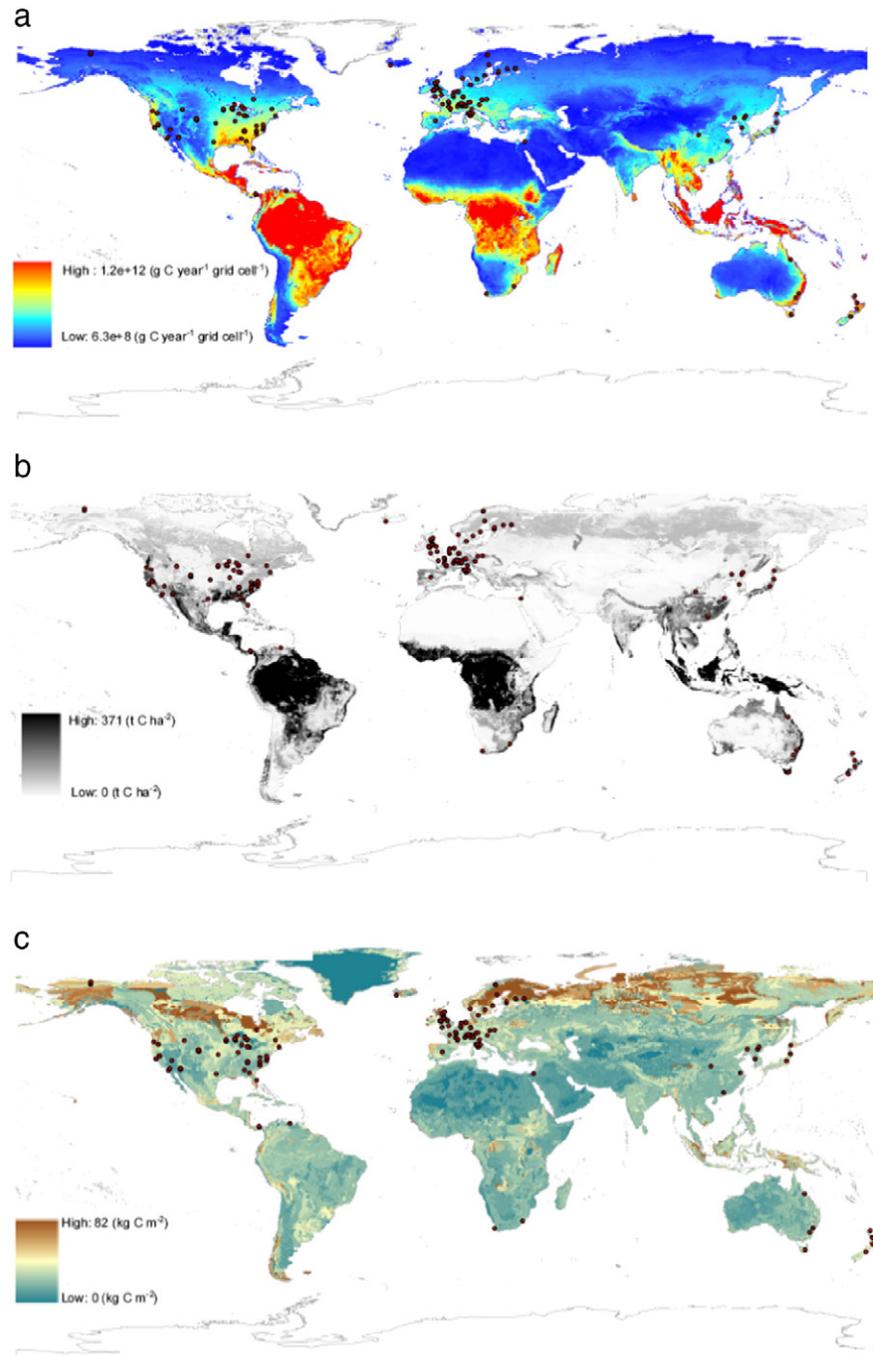


Fig. 1. Locations of all eCO_2 experiments (red markers) investigating effects on natural ecosystem functioning worldwide since 1987, plotted against globally modeled relative values for: (a) net primary productivity (NPP) ($g\ C\ ha^{-1}\ year^{-1}$) (data: Imhoff and Bounoua, 2006), (b) above- and below-ground living carbon density (at differing soil depths according to location) ($t\ C\ ha^{-1}$) (data: Ruesch and Gibbs, 2008), (c) soil carbon density (to 1 m depth) ($kg\ C\ m^{-2}$) (data: Matthews et al., 2000).

have been extensively studied under eCO_2 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 eCO_2 sink capacity, either individually or in combination. Addressing the influence of factors such as these alongside eCO_2 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 CO_2 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 eCO_2 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 eCO_2 , remains a research priority. It is uncertain whether increased C sequestration will occur with eCO_2 conditions and under a warming atmosphere. However, we need to establish if the addition of new carbon,

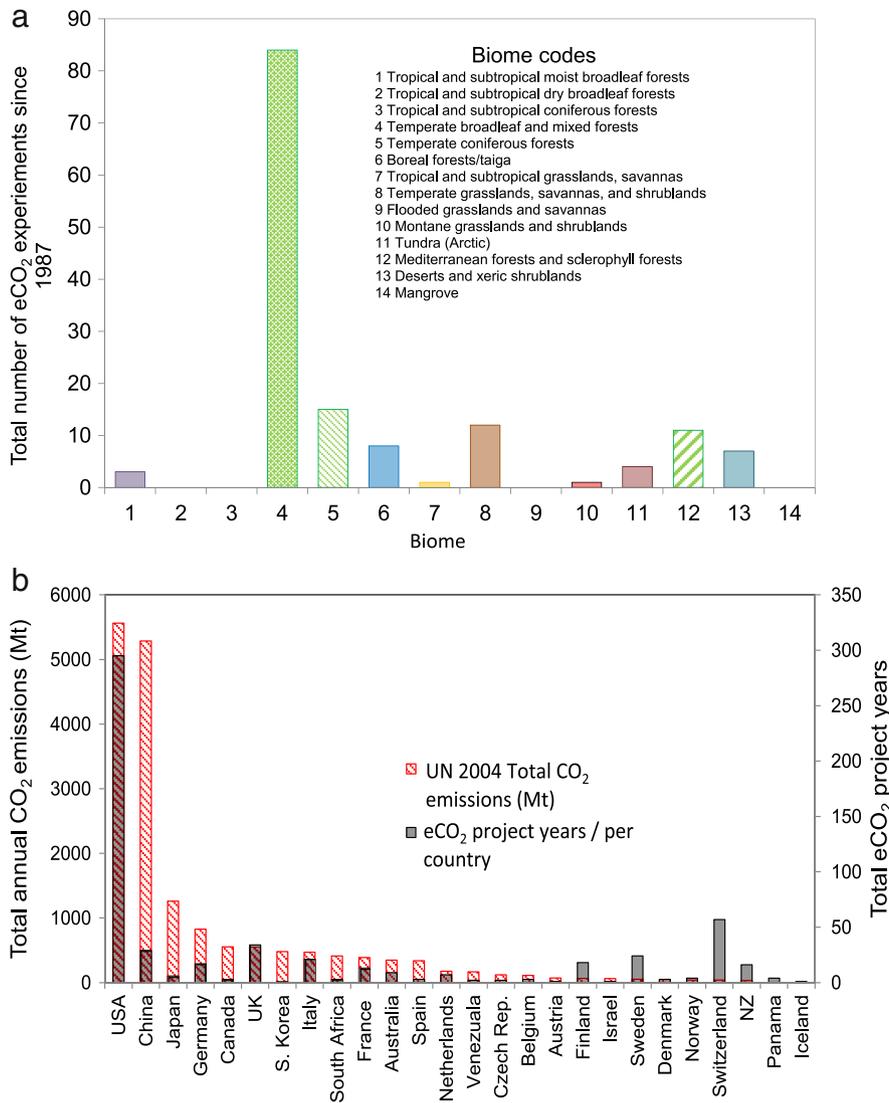


Fig. 2. a) Numbers of eCO₂ experiments per biome (according to Olson et al., 2001 biome definitions), since 1987 shown in colored boxes and b) total annual CO₂ emissions per country against relative levels of investment in eCO₂ research, derived from the total number of experimental project years per country. According to the top 25 ranked CO₂ emitters worldwide for 2004 (source: CIDAC, 2012).

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 (Marthews 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

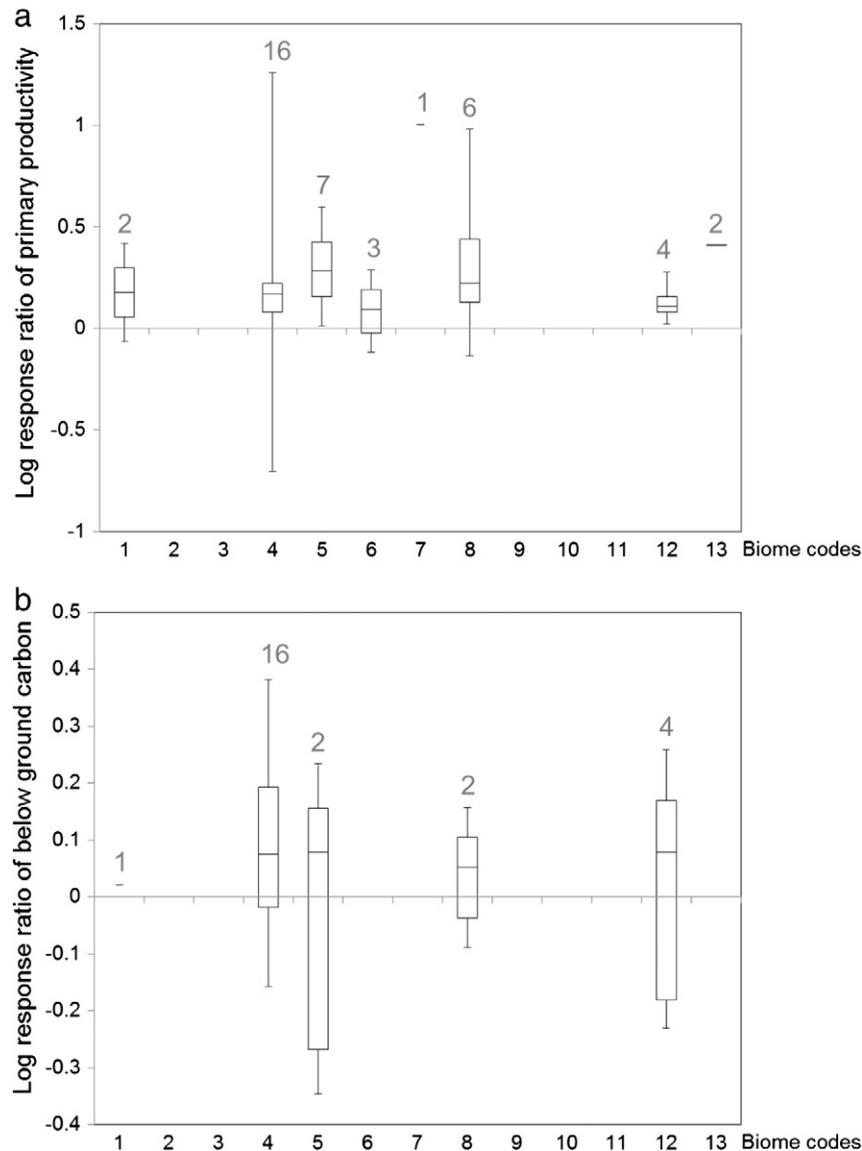


Fig. 3. Box and whisker plots showing the median, median and quartile range of log response ratios, according to each biome, calculated from experimental differences between eCO₂ and ambient CO₂ treatments for a) primary productivity ($n = 41$) and b) soil carbon ($n = 26$). Soil carbon values were for total or organic carbon (between 0 and 30 cm depths). Where equivalent data from multiple years existed from a single experiment, the latest values (i.e. those arising near the end of experimentation) were used. The figures above each data point indicate the numbers of experiments per biome used to derive each box and whisker plot. Biome codes are as given in Figure 2a.

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 \times 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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