Viewpoints

Model–data synthesis for the next generation of forest free-air CO_2 enrichment (FACE) experiments

Summary

The first generation of forest free-air CO_2 enrichment (FACE) experiments has successfully provided deeper understanding about how forests respond to an increasing CO_2 concentration in the atmosphere. Located in aggrading stands in the temperate zone, they have provided a strong foundation for testing critical assumptions in terrestrial biosphere models that are being used to project future interactions between forest productivity and the atmosphere, despite the limited inference space of these experiments with regards to the range of global ecosystems. Now, a new generation of FACE experiments in mature forests in different biomes and over a wide range of climate space and biodiversity will significantly expand the inference space. These new experiments are: EucFACE in a mature *Eucalyptus* stand on highly weathered soil in subtropical Australia; AmazonFACE in a highly diverse, primary rainforest in Brazil; BIFoR-FACE in a 150-yr-old deciduous woodland stand in central England; and SwedFACE proposed in a hemiboreal, *Pinus sylvestris* stand in Sweden. We now have a unique opportunity to initiate a model–data interaction as an integral part of experimental design and to address a set of cross-site science questions on topics including responses of mature forests; interactions with temperature, water stress, and phosphorus limitation; and the influence of biodiversity.

Introduction

The exchange of CO_2 between the atmosphere and the terrestrial biosphere is an important controller of atmospheric CO_2 concentration and hence the global climate. A prominent and unsettled question is to what degree plant CO_2 uptake will be stimulated by an ever-increasing atmospheric CO_2 concentration, providing negative feedback and moderating the progression of climate change (Arora *et al.*, 2013; Friedlingstein *et al.*, 2014). The free-air CO_2 enrichment (FACE) experiments that were conducted in several forested research sites from *c.* 1996 to *c.* 2010 have proven to be a valuable source of understanding and data on the responses of forest ecosystems to a future CO_2-enriched atmosphere (Nowak *et al.*, 2004; Ainsworth & Long, 2005; Norby *et al.*, 2005; Hyvönen *et al.*, 2007; Norby & Zak, 2011). There are few alternative approaches to explore ecosystem-scale responses to CO_2 enrichment over relevant spatial and temporal scales, given the size and lifespan of trees. Although forest FACE experiments can be difficult and expensive to construct and operate, they provide an opportunity for a comprehensive approach that integrates multiple process-level investigations on carbon (C), water, and nutrient fluxes and their responses to elevated CO_2 (eCO_2) under the influence of fluctuating weather.

Despite the considerable advances of FACE experiments over earlier experiments with tree seedlings in growth chambers and saplings in open-top chambers (Norby *et al.*, 1999), FACE experiments, past or future, still represent a small fraction of the life of a tree and the spatial extent and diversity of forests. To address the critical issues associated with forest responses to rising atmospheric CO_2 concentration and the feedbacks provided to the climate system, we must rely on models that simulate the exchange of C, water, and energy in the terrestrial biosphere. Model predictions of responses to eCO_2 should correspond with, or at least be informed by, the responses observed in FACE experiments. The FACE model–data synthesis (FACE-MDS) project (Walker *et al.*, 2014) challenged 11 terrestrial ecosystem models with data from the Oak Ridge National Laboratory FACE experiment (ORNL FACE) in Tennessee, USA, and Duke FACE in North Carolina, USA. This exercise was valuable in identifying critical model assumptions and evaluating whether the assumptions were supported by the data (De Kauwe *et al.*, 2013, 2014; Zaehle *et al.*, 2014; Medlyn *et al.*, 2015), and it provided a framework to evaluate forest processes that occur over much longer time frames (> 100 yr) than the duration of the experiments (Walker *et al.*, 2015). The FACE-MDS project extended the value of the two FACE experiments and helped them to fulfill their original objectives of understanding the integrated responses of intact forest ecosystems to CO_2 enrichment of the atmosphere and the feedbacks from the forest to the atmosphere.

A challenge for informing global terrestrial ecosystem models with FACE data has been the limited global representativeness of the first generation FACE experiments, as the forest experiments were conducted in the temperate zone (Hickler *et al.*, 2008; Baig *et al.*, 2015). Mooney *et al.* (1991) recommended more than two decades ago that, at a minimum, ecosystem-level experiments on effects of eCO_2 be undertaken in each of the world's six major biomes: tundra, boreal forest, temperate forest, tropical forest, grassland, and desert. The next generation of forest FACE experiments will greatly expand the breadth of our knowledge base on responses to elevated CO_2 by addressing responses of mature forest ecosystems in different biomes over a wide range of climatic and edaphic conditions (Fig. 1; Table 1). These new experiments include EucFACE, situated in a mature *Eucalyptus* forest in Australia (already underway); AmazonFACE, located in an old-growth tropical rainforest in Brazil and BIFoR-FACE, set in

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Fig. 1 The four new free-air CO_2 enrichment (FACE) sites are all in mature forests, but they differ considerably in stand structure and biodiversity. (a) EucFACE (Australia); (b) AmazonFACE (Brazil); (c) BIFoR-FACE (United Kingdom); (d) SwedFACE (Sweden).

an old oak woodland in England (both under construction); and a proposed experiment in a pine forest in southern Sweden (SwedFACE). Some important and intriguing science questions could not be addressed in the first generation of FACE experiments and can be answered only in mature forests over a wide range of environmental conditions. These questions, which we discuss herein, are critical for improving terrestrial ecosystem and Earth system models. Here, we describe the next generation of forest FACE experiments and propose a set of model-guided, cross-site science questions that will set a research agenda for the next decade.

Model–experiment interaction

Historically, modeling of experimental results began at the conclusion of the experiment, as was the case with the first generation of FACE experiments, but our experience with the FACE-MDS project has clearly shown the value of initiating the model–experiment interaction early on as the experiment is first being designed (Medlyn *et al.*, 2015). This interaction adds value to both the experiment and the modeling.

How can modeling inform FACE experiment development?

Models provide a global context for FACE experiments. Well before any FACE experiments had been initiated, Mooney *et al.* (1991) used a conceptual model to generate predictions of the relative response of different ecosystems to eCO_2 in relation to prevailing nutrient and water availability (Fig. 2). In their scheme, the Amazon forest and the Swedish pine forest would be predicted to have a smaller response to eCO_2 than the *Eucalyptus* forest or temperate deciduous forests. Employing a model including improved process understanding, Hickler *et al.* (2008), suggested that the eCO_2 response of productivity should increase from boreal to temperate and tropical ecosystems as consequence of the biochemistry of photosynthesis (see Temperature section later).

Ecosystem models can inform FACE experiment development by assisting with the formulation and refinement of testable hypotheses (Norby & Luo, 2004), for example, alternate predictions from competing hypotheses on how responses to eCO_2 vary with temperature and water availability (Luo *et al.*, 2008). Modeling specific FACE experiments at their outset can provide testable predictions against which hypotheses can be examined (e.g. Parton *et al.*, 2007; Dijkstra *et al.*, 2010), and can inform FACE experimental design (e.g. whether to include factorial nutrient or water treatments). Model parameter sensitivity analysis can identify key parameters and processes that strongly affect the predicted ecosystem response and thereby ensure that appropriate measurements are made and that data are presented and preserved in a common format with robust meta-data.

Data assimilation, that is the systematic optimization of model parameters and state-variables to match measured ecosystem observations, can be used to estimate unmeasured ecosystem properties such as C pools and fluxes. Such state and parameter estimations can build a more complete picture of the experiments and thereby can help to develop or test specific hypotheses, for example the likely destination of additional fixed photosynthate. One particular important application of data assimilation is to synthesize multiple data streams to help assessing data quality and internal consistency by synthesizing multiple sets of measurements (e.g. photosynthesis, growth, soil respiration).

The application of a multi-model ensemble to FACE sites also provides an opportunity to identify important observables (Medlyn *et al.*, 2015), which would help to judge the adequacy of competing hypotheses. For example, De Kauwe *et al.* (2013) showed that the

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Table 1 Characteristics of new forest free-air CO_2 enrichment (FACE) experiments

	AmazonFACE	EucFACE	BIFoR-FACE	SwedFACE (proposed)
Location	North of Manaus, Brazil	Richmond, New South Wales, Australia	Staffordshire, Central England, UK	Southern Highlands, Sweden
Latitude, longitude	−2.596°, −60.208°	−33.618°, 150.738°	52.801°,−2.301°	57.167°, 14.783°
Climatic zone	Tropical	Subtropical	Temperate	Hemi-boreal
Vegetation type	Broadleaf evergreen rainforest	Dry *Eucalyptus* forest	Deciduous coppice-with-standards woodland	Boreal conifer forest
Primary species	Highly diverse	*Eucalyptus tereticornis*	*Quercus robur*, *Acer pseudoplatanus*, *Betula pendula*. Understory: *Corylus avellana*, *Ilex aquifolium*	*Pinus sylvestris*
Average canopy height (m)	30 m	22 m	25 m	12–15 m
Canopy tree age (yr)	> 200	> 100	Standards: *c.* 150 yr Coppice poles: > 20 yr	34
Soil type (USDA/FAO)	Oxisol Xanthic Ferralsol	Entisol Orthic Acrisol	Entisol Orthic Luvisol	Spodosol Haplic podsol
MAT (°C)	26.7	17.2	9	5.5
MAP (mm)	2400	800	690	688
PET (mm)	1616	1357	641	620
Growing season length (d)	365	365	275	190
Number of plots	2, expanding to 8	6	9	6
Plot diameter (m)	30 m	25 m	28 m	25 m
CO_2 treatment levels	Ambient + 0, ambient + 200 ppm	Ambient + 0, ambient + 150 ppm	Ambient, ambient + 0, ambient + 150 ppm	Ambient, ambient +150 ppm
Treatment start date	December 2016	September 2012	April 2016	Planned April 2017
Website	https://www.inpa.gov.br/amazonface/	http://www.uws.edu.au/hie/facilities/EucFACE	http://www.birmingham.ac.uk/bifor	

Soil type given both as United States Department of Agriculture (USDA) classification and the Food and Agriculture Organization (FAO) of the United Nations classification. MAT, mean annual temperature; MAP, mean annual precipitation; PET, potential evapotranspiration, which comes from http://www.cgiar-csi.org/data/global-aridity-and-pet-database. Growing season is defined as number of days between average date of last and first frost of the years.

decoupling coefficient (a measure of how well canopies are coupled to the atmosphere) strongly affects the response of ecosystem water-use efficiency to eCO_2; hence, this coefficient should be estimated in FACE experiments to better understand and interpret the ecosystem's CO_2 response.

How can FACE experiments inform models?

Using observations from FACE experiments to evaluate ecosystem models is challenging: it is not simple to disentangle quantitatively the direct effect of eCO_2 on ecosystem processes from other ecosystem dynamics, as specific site properties and history can confound any signal at the ecosystem level. The direct use of the emergent ecosystem-level response (e.g. the net primary production (NPP) response to eCO_2) as a quantitative constraint for ecosystem models is therefore limited in the power to constrain a particular ecosystem model, or to discriminate between competing ecosystem models (Hickler *et al.*, 2008; Zaehle *et al.*, 2010; Piao *et al.*, 2013; Walker *et al.*, 2014). The assumption-centered analytical approach employed by the FACE-MDS has successfully overcome this divide by testing the validity of the model's assumptions on ecosystem response to eCO_2 at the level of the underlying processes (Medlyn *et al.*, 2015). This approach consists of defining a conceptual framework, which splits the emergent ecosystem level response (e.g. NPP) into independently observable, contributing process responses (e.g. nutrient uptake and nutrient-use efficiency), identifying suitable and independent observations to constrain these processes, and linking these observables to model output. The assumption-centered approach allows models to benefit from the data richness of FACE experiments but requires a high level of harmonization of model inputs and outputs, and an assessment of the degree to which observed and modeled quantities are comparable. The approach facilitates the identification of preferable hypotheses at the level of model components rather than the emergent model behavior, and thereby provides a stronger evaluation of a model's adequacy to model eCO_2 responses, even if the emergent response at ecosystem level remains uncertain. Where largely divergent model responses remain unconstrained from observations, the approach identifies the potential for additional measurements, or the maximum level of measurement error

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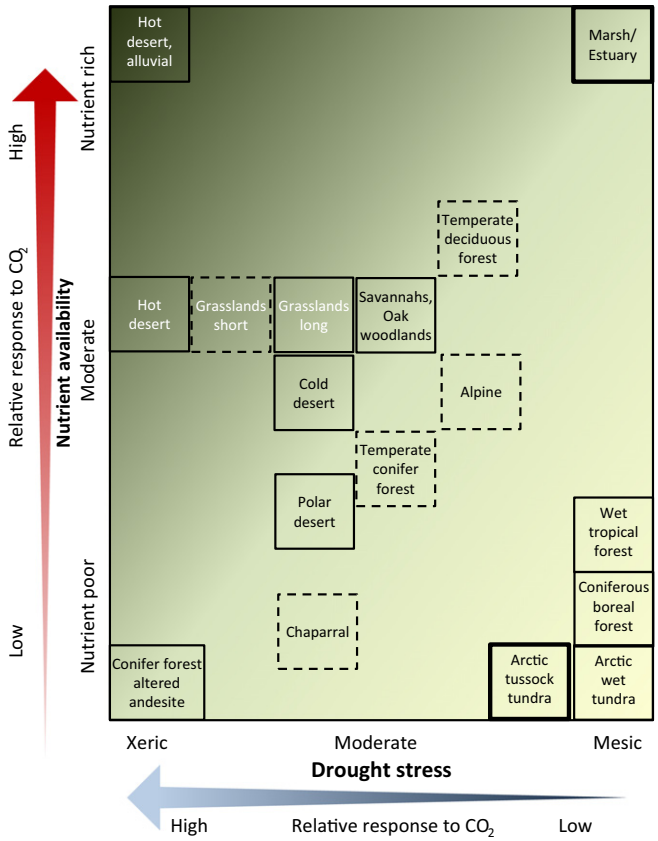

Fig. 2 Hypothesized response of ecosystems to elevated CO_2 (eCO_2) in relation to prevailing nutrient and water availability, redrawn from Mooney *et al*. (1991). When this figure was generated, only two ecosystems (marked in heavy outlines) had been studied in the field; those outlined in dashes had been studied in controlled environment chambers, and those ecosystems outlined by thin lines had not yet been studied in 1991. Since that time, field studies, including free-air CO_2 enrichment (FACE) experiments, have been conducted in many of the other ecosystems, including desert, grasslands, chaparral, alpine, and temperate deciduous forest, but no FACE experiments have yet been conducted in tropical forests or coniferous boreal forests. Increasing green color indicates greater relative response to eCO_2, based on the assumptions that response increases with drought stress and with nutrient availability.

tolerable, to successfully discriminate between competing model hypotheses.

The next generation of FACE experiments

The next generation of FACE experiments provides an unprecedented opportunity to put the concepts of model–experiment interaction described earlier to use. The four experiments we describe will greatly expand the ecological, geographical, and climatic range of the inference sphere of forest responses to elevated CO_2. The new studies are located in boreal, temperate, subtropical, and tropical regions, and unlike the first generation of FACE experiments, all are in mature forests (Table 1). By initiating model–experiment interactions at the early stages of planning and implementation of the experiments, modeling can be used to guide the experimental design, as described earlier, and optimize the eventual use of experimental data to test and inform models.

EucFACE

The EucFACE experiment is located on the Cumberland Plain in subtropical Australia on a highly weathered soil with low phosphorus (P) availability (Crous *et al*., 2015). The remnant, native, sclerophyll woodland of 22 m tall *Eucalyptus tereticornis* trees is an open stand (leaf area index (LAI) < 2), with C_3 and C_4 grasses and herbaceous plants in the understory (Fig. 1a). The forest is unmanaged except perhaps for firewood cutting > 50 yr ago. The overarching experimental objective is to address the potential for sustained C accumulation in trees and soils on nutrient-limited sites. Key questions being asked are: does CO_2 enrichment stimulate ecosystem C storage in a P-limited woodland? What are the interactions between C cycling and nutrient availability on highly-weathered soils? The experiment was conceived to address the hypothesis that on P-limited sites, extra C allocated belowground as extracellular organic acids can help liberate P and sustain moderate growth enhancement from CO_2 enrichment, although enhanced photosynthetic rates may not be fully sustained over time. A second emphasis at this site is associated with the periodic droughts experienced in subtropical to temperate regions. Potential evapotranspiration (PET) exceeds mean annual precipitation (MAP) at this site by > 50% (Table 1), and thus water deficits are common. A third research question of the experiment is if eCO_2 drives ecosystem water savings to such an extent that there is increased C storage in vegetation in elevated CO_2 in seasonally-dry woodland. The experiment was initiated in September 2012, by gradually ramping up the CO_2 concentration to ultimately reach an experimental target of ambient + 150 ppm in three of the six 25-m diameter plots. EucFACE uses a pre-dilution CO_2 fumigation system (Lewin *et al*., 2009), as will the other experiments described here.

AmazonFACE

The AmazonFACE experiment is being developed in a highly diverse, old-growth, closed canopy *terra firme* forest on a plateau within the Amazon River basin 70 km north of Manaus, Brazil (Fig. 1b). The experiment is intended to help answer the overarching question: how will rising atmospheric CO_2 affect the resilience of the Amazon forest, the biodiversity it harbors, and the ecosystem services it provides (Lapola & Norby, 2014)? It is the first time a FACE experiment will be conducted in a tropical forest, despite the long-standing recognition in science (e.g. Mooney *et al*., 1991; Cernusak *et al*., 2013) and policy communities (e.g. Vergara & Scholz, 2011) of the need for such an experiment. In addition to the significant challenges presented by the remoteness of the site and the tropical environment, the stature of the forest (*c*. 30 m) and its very high plant diversity are significant features controlling sampling designs. Initial surveys indicate that two 30-m diameter plots include at least 21 different families and 52 species of trees with diameters > 10 cm; only 10 families and five species were represented in both plots. Although this census represents a very small fraction of the estimated 16 000 tree species in Amazonia (ter Steege *et al*., 2013), the biodiversity of the experimental plots greatly exceeds that of other forest FACE experiments. Before the experimental treatment, relevant C, water and nutrient fluxes and

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stocks will be monitored from eight circular plots (30 m diameter) at the research area for a period of 2 yr (started in December 2014). Two plots (control and treatment) will then have the infrastructure for CO_2 fumigation implemented, and a pilot experiment will run for another 2 yr. The full implementation of the AmazonFACE experiment (four control plots and four treatment plots) will run continuously for 10 yr after the pilot experiment.

BIFoR-FACE

The Birmingham Institute of Forest Research (BIFoR) FACE is a CO_2 enrichment experiment in a mature deciduous temperate woodland on long-established woodland soil (Fig. 1c). The BIFoR-FACE woodland site is a coppice-with-standards English oak (*Quercus robur*) woodland (Rackham, 2008) with predominantly hazel (*Corylus avellana*) coppice, which through lack of management has grown tall with many closely spaced stems and little ground vegetation ($5 < LAI < 7$). The oaks were planted *c.* 150 yr ago; other species have self-seeded and become established, particularly sycamore (*Acer pseudoplatanus*), silver birch (*Betula pendula*), and holly (*Ilex aquifolium*), leading to a distribution of ages in dominant and sub-dominant trees at the site. The site, therefore, provides an opportunity to assess the differential response between oak and sycamore standards and between the main canopy and the coppice understory. Substantial amounts of deadwood are present, as standing deadwood, fallen stems, and coarse woody debris. MAP and PET are approximately in balance in the long-term mean (Table 1), but seasonal and sub-seasonal droughts do occur. The FACE experiment is designed to address the following top-level research questions: does elevated CO_2 increase the C storage in a mature temperate deciduous woodland ecosystem (cf. Luyssaert *et al.*, 2010)? Do other macro- or micronutrients limit the uptake of C in this ecosystem now, or are they likely to in the future? What aspects of biodiversity and ecosystem structure and function alter under eCO_2, and how do these alterations feed back onto C storage? BIFoR-FACE began in summer 2014 to characterize the site ahead of installation of the FACE infrastructure. CO_2 fumigation is planned to begin in spring 2016. In order to separate transient responses from sustained long-term responses, the FACE experiment is designed to run for more than a decade.

SwedFACE

SwedFACE is a proposed multi-factor ecosystem manipulation experiment that will be implemented in a *c.* 35-yr old closed-canopy stand of mature Scots pine (*Pinus sylvestris*) trees in the hemiboreal zone of southern Sweden (Fig. 1d). The stand was probably subjected to noncommercial thinning some time before canopy closure, but it is currently unmanaged. The project aims to bridge the knowledge gap left by past forest FACE experiments as to the direct effects of rising CO_2 concentrations on boreal forests, focusing on belowground processes and nutrient feedbacks that may counteract the primary plant physiological responses to eCO_2. Boreal forests are an important reservoir for stored C and may in the future contribute increasingly to biosphere–atmosphere C exchange as higher average temperatures lead to an extension of the growing season, promoting C uptake, and faster decomposition rates, promoting C release from warming soils. The SwedFACE experiment will comprise crossed $CO_2 \times$ nutrient treatment, with supplementary manipulations in an adjacent stand to address single-factor responses to nitrogen (N), P, multiple nutrients and irrigation.

Cross-site research questions

Each of these independent experiments will have a set of science questions and hypotheses that are unique to the site and to the interests of the researchers and funding agents involved. There also are some compelling questions that are common to all of these sites and will benefit from a cross-site analysis. These cross-site questions are the ones we describe here, with the intention of organizing and stimulating the science community to establish common protocols and model frameworks to best exploit this unique opportunity.

Mature forests

A question of fundamental importance to global change research is: Will increased atmospheric CO_2 lead to increased biomass in mature forest systems? A large volume of research has been devoted to measuring changes in aboveground forest biomass and attributing these changes to environmental change (e.g. Pan *et al.*, 2011; Brienen *et al.*, 2015). Increasing CO_2 has been implicated as the most likely cause of increasing biomass in many forest ecosystems (Schimel *et al.*, 2015), but this is the topic of much debate, and several tree-ring studies have indicated increased water use efficiency (WUE) but not growth (Peñuelas *et al.*, 2011; Silva & Anand, 2013; van der Sleen *et al.*, 2014). In the WebFACE experiment (Bader *et al.*, 2010), individual trees in a mature, mixed-deciduous forest in Switzerland had similar leaf-level physiological responses to eCO_2 to those observed in younger, plantation forests, but ecosystem-scale C budgets are difficult to determine or evaluate from individual tree exposures. Forest stand-level exposures to eCO_2 are needed to evaluate whether stimulation of productivity, including belowground productivity, will depend on the factors limiting growth such as soil nutrients and water, and whether feedbacks through increased C assimilation or WUE can help to overcome these limiting, or co-limiting, factors.

Biomass was increased by eCO_2 in several forest FACE and open-top chamber experiments (McCarthy *et al.*, 2010; Hungate *et al.*, 2013; Talhelm *et al.*, 2014), but these forests were aggrading or disturbed, and the observed increases in biomass may represent only an accelerated approach to an equilibrium that is common to both ambient CO_2 and eCO_2 (Fig. 3). The new forest FACE experiments described earlier are in mature forests and, except for the single-aged pine stand in SwedFACE, presumed to be close to a quasi-equilibrium state. To the best of our knowledge there has been only minimal disturbance in the past several decades. Soil organic matter and nutrient cycling are likely to be more coupled to the vegetation in these mature ecosystems than in the first-generation forest FACE experiments in forests planted on agricultural soils, thereby improving our knowledge and modeling of the coupling between C and nutrient cycling (Zaehle *et al.*, 2014).

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Models tend to predict a shift in allocation towards wood, which decreases overall C turnover rates (De Kauwe *et al.*, 2014; Walker *et al.*, 2015). Models that emphasize changes in nutrient limitations during stand development also predict increased allocation to fine roots (McMurtrie *et al.*, 2012; Farrior *et al.*, 2013; De Kauwe *et al.*, 2014). Allocation to reproductive structures is likely to comprise a substantial proportion of production in mature stands, and the effects of eCO_2 on fecundity and the stoichiometry of reproduction will be important features of the response of these mature systems that were mostly missing from previous forest FACE experiments.

Key questions for these mature ecosystems are: will stimulated photosynthesis and increased WUE result in stimulated productivity? How will allocation and tissue turnover rates respond to eCO_2?

Nutrient limitation

Predicting ecosystem responses to eCO_2 requires quantitative understanding of nutrient cycling processes and their interactions with C and water cycling. First generation FACE experiments were located in temperate ecosystems, which are predominantly N-limited. These experiments have provided evidence of nutrient feedbacks both dampening the CO_2 fertilization response of tree growth through accelerated decline in N availability (Norby *et al.*, 2010), and sustaining growth responses to eCO_2 through enhanced nutrient liberation from soil organic material caused by accelerated C cycling through the root–microbe–soil system (Drake *et al.*, 2011; van Groenigen *et al.*, 2014).

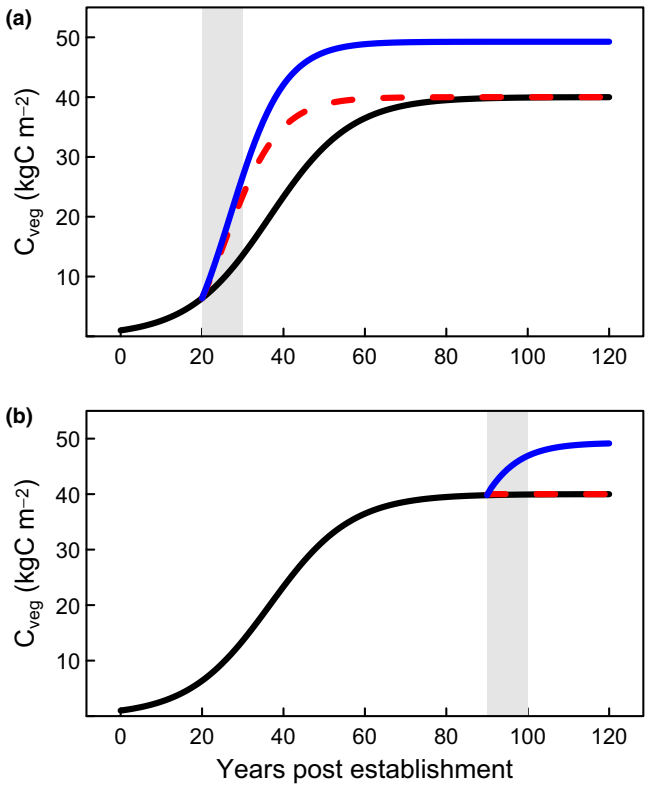

Fig. 3 Simplified forest biomass accumulation curves under ambient (black) and elevated CO_2 (eCO_2; red and blue) illustrating two hypotheses of vegetation carbon (C_{veg}) response to eCO_2. The red hypothesis is that eCO_2 elevates growth rates but does not increase equilibrium biomass. The blue hypothesis is that eCO_2 elevates both growth rates and equilibrium biomass. Previous forest free-air CO_2 enrichment (FACE) experiments (a) were in aggrading ecosystems, and it was not possible to distinguish between the two hypotheses during the course of the experiment (gray bar). The new FACE experiments described in this paper, are in mature forests and, except for the single-aged pine stand in SwedFACE, are presumed to be close to a quasi-equilibrium state; the distinction between the two hypotheses during the experiment (gray bar) is clear (b).

While there is a growing body of knowledge on N cycle interactions with eCO_2 on forest growth in boreal and temperate systems on relatively young soils (for example, Norby *et al.*, 2010; Drake *et al.*, 2011; Hungate *et al.*, 2013), there is very little knowledge regarding the interaction of nutrient cycling with eCO_2 on highly weathered soils with low plant-available P contents. Limited P and N availability are likely jointly to impact C storage by forests and other natural ecosystems (Peñuelas *et al.*, 2013). Phosphorus limitation is widespread in old growth forests that reside on P-impoverished soils, such as those in large parts of South America, Africa, southeast Asia, and Australia (Fig. 4). The few field investigations of the effect of eCO_2 on P availability have given mixed results (Johnson *et al.*, 2003; Khan *et al.*, 2008), and the possibility of eCO_2 to liberate P and thus lift P-limitation has received little attention. This lack of understanding and observations on the effects of P limitation is a major challenge for the increasing number of land surface models that are incorporating P dynamics (Wang *et al.*, 2007, 2010; Goll *et al.*, 2012; Yang *et al.*, 2014; Reed *et al.*, 2015). For example, model sensitivity experiments have shown that both phosphatase activity and phosphate sorption kinetics can significantly affect P availability and determine whether or not ecosystem response to eCO_2 will be sustained (Goll *et al.*, 2012; Yang *et al.*, 2014).

Based on their geographical location and local soil, the four new FACE sites are thought to differ considerably in their N and P availabilities. Simulations with CLM-CNP (community land model with coupled carbon, nitrogen, and phosphorus cycles) (Yang *et al.*, 2014) were used to estimate the global distribution of the degree of N vs P limitation on productivity, based on the ecosystem demand for these nutrients in relation to their supplies (Fig. 4). Testing the predictions for the four FACE sites resulting from this analysis provides a unique opportunity to develop relationships between plant traits, nutrient cycling processes, and responses to eCO_2 across a wide range of environmental conditions. The resulting data sets will be all the more powerful if coupled with insights coming from tropical forest fertilization experiments, soil warming experiments, and other ongoing efforts to quantify the plant–soil interactions that control nutrient availability and uptake (Reed *et al.*, 2015), especially if common measurement protocols are adopted across all of these studies.

For the new set of FACE experiments, the overarching question from the nutrient perspective is whether nutrient limitation, in particular P, will preclude ecosystem response to eCO_2. To answer this question requires understanding the effect of eCO_2 on processes in four major areas: the flexibility of C : N : P stoichiometry in vegetation and soil; plant P acquisition strategy; microbial dynamics; and soil mineral P availability.

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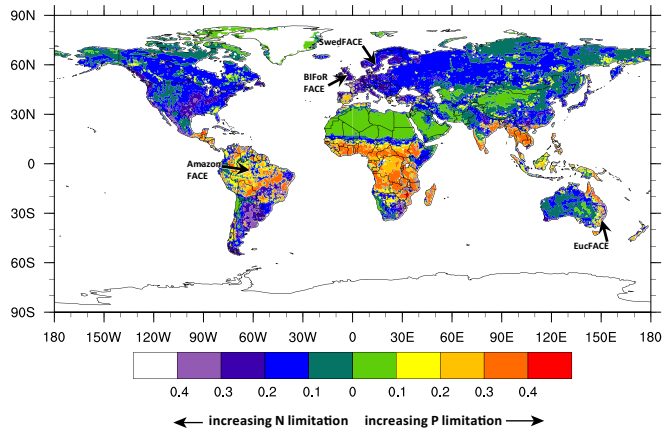

Fig. 4 Simulated spatial variation of nutrient limitation (nitrogen (N) and phosphorus (P)) on the global scale using CLM-CNP (Yang *et al.*, 2014). Values plotted are the proportion by which plant growth is reduced due to limitation of that nutrient, following Wang *et al.* (2010): $1 - f^{P}_{plant}$ when $f^{P}_{plant} < f^{N}_{plant}$ and $1 - f^{N}_{plant}$ when $f^{N}_{plant} < f^{P}_{plant}$, where f^{P}_{plant} is the limitation factor on plant growth considering P supply and demand, while f^{N}_{plant} is the limitation factor on plant growth considering N supply and demand (Yang *et al.*, 2014).

Temperature

Another longstanding unresolved question relates to the interaction of rising CO_2 concentration with temperature. Long (1991) showed that the effect of high CO_2 on photosynthesis should be higher at high temperature, owing to the kinetics of the Rubisco enzyme. This interaction is captured in ecosystem models that incorporate the Farquhar *et al.* (1980) model of photosynthesis, which is common to most existing global models (e.g. Zaehle & Dalmonech, 2011). Such models predict that canopy photosynthesis will have a higher temperature optimum under eCO_2 (McMurtrie & Wang, 1993). This interactive effect on gross photosynthesis typically flows through to NPP such that ecosystem models often predict that the CO_2 response will be larger in tropical than temperate or boreal ecosystems (e.g. Hickler *et al.*, 2008); and that rising global temperatures will amplify the response to the increase in atmospheric CO_2 concentration (e.g. Medlyn *et al.*, 2011).

Recent cross-site comparisons for the interaction between CO_2 and temperature comparisons are equivocal. Many factorial CO_2 × temperature experiments fail to find a positive interaction (e.g. Teskey, 1997; Norby & Luo, 2004; Sigurdsson *et al.*, 2013), and meta-analyses of such experiments do not find that the CO_2 response is higher at higher growth temperatures (Dieleman *et al.*, 2012; Wang *et al.*, 2012; Baig *et al.*, 2015). Baig *et al.* (2015) compiled growth responses from all field-based elevated CO_2 experiments with woody species carried out to date, and tested for a relationship with mean annual temperature. Owing to high variability across experiments, the confidence bands on the relationship were wide, and included both possibilities of no interaction, and an interaction of the size predicted by three vegetation models. Thus, this question is unable to be resolved with existing data. However, most experiments to date have been carried out in the temperate zone, and there is a critical lack of data from boreal and tropical environments. The new FACE experiments cover a natural temperature gradient (mean annual temperature: 5.5°C, 9°C, 17°C, 27°C; Table 1) and thus provide an exciting opportunity to use cross-site comparisons to address this question.

Will the response of NPP to CO_2 across these experiments increase with growth temperature as the models currently predict? Importantly, if no such interaction is found, we will need to identify the mechanisms responsible, so that the models can be correctly modified. This can be achieved by careful testing of the underlying processes in the models using cross-site data. We will need to know whether the CO_2 response of leaf photosynthesis is higher at warmer sites, as the models predict. Alternatively, leaf-level acclimation to temperature (Gunderson *et al.*, 2010), or changes in leaf temperature as a result of reduced stomatal conductance under eCO_2 (Warren *et al.*, 2011b) could potentially negate this interaction. We will also need to know whether an interaction at leaf scale flows through to an interaction on NPP, or whether feedbacks through other processes such as respiration, water use, or nutrient cycling offset any potential interaction. Integration of models into cross-site comparisons thus provides a major opportunity to resolve this long-standing question.

Water stress

The current global knowledge base from eCO_2 experiments suggests that increased WUE due to eCO_2 could partially alleviate effects of water stress on productivity except when water availability is below a certain threshold (Morgan *et al.*, 2004; Nowak *et al.*, 2004). The interaction between $[CO_2]$ and water stress is pertinent because it has long been assumed that eCO_2 reduces the impact of drought, leading to a higher CO_2 effect on productivity under soil water stress (Wullschleger *et al.*, 2002). This presumed CO_2 × drought interaction was a basis for predictions of relative response of different ecosystems to eCO_2 (Mooney *et al.*, 1991; Fig. 2). Also, eCO_2 may be able to increase C reserves or delay the onset of drought (Morgan *et al.*, 2011; Hovenden *et al.*, 2014), which could lead to increased forest resilience, and reduced mortality, during periods of episodic drought.

Model studies (Duursma & Medlyn, 2012) predict this interaction primarily as a consequence of lower stomatal conductance (g_s) in eCO_2 leading to higher soil water content (SWC), thus reducing the impact of drought on productivity. Although reduced g_s has indeed been observed in forest FACE sites (Ainsworth & Long, 2005; Warren *et al.*, 2011a), support for a follow-on effect on SWC in forest ecosystems has been mixed (Gunderson *et al.*, 2002; Wullschleger *et al.*, 2002), although SWC measurements were usually made only on near-surface soil. Furthermore, while eCO_2 can reduce water loss under drought conditions, excessive stomatal closure brought on by acute drought can offset the benefits of eCO_2 for C assimilation. For example, in ORNL FACE, stomatal closure in eCO_2 reduced evaporative cooling resulting in premature leaf senescence during an extreme drought and heat wave (Warren *et al.*, 2011b). The lack of a clear CO_2 × drought interaction in previous FACE sites is likely due to other factors affected by eCO_2, including increased LAI (Norby & Zak, 2011; Tor-ngern *et al.*, 2015), deeper

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roots (Iversen, 2010), and changes in plant hydraulic conductance (Domec *et al.*, 2009). Another important interaction is nutrient availability, which is also affected by water limitation (Kreuzwieser & Gessler, 2010), potentially reducing the CO_2 effect on productivity during drought due to nutrient limitations, or reducing nutrient availability in periods of high water availability due to leaching (Hovenden *et al.*, 2014). It is thus necessary to study the interactions between acclimation of vegetation properties to eCO_2 and the response of nutrient cycling to water availability to fully characterize the $CO_2 \times$ drought interaction.

Although the four new forest FACE experiments are in locations that vary in MAP by 3.5 fold, and in moisture index (MAP/PET) by 2.5 fold (Table 1), it will not be possible to ascribe differences among experiments in system-level responses (e.g. NPP) strictly to differences in water regime, given confounding differences in soil, climate, and vegetation. Nevertheless, the range in water regimes creates an opportunity for testing model assumptions about differences in plant traits and their impact on the CO_2 effect on WUE (De Kauwe *et al.*, 2013). There may also be opportunities to compare how eCO_2 alters responses to periodic droughts that may occur sometime during the 10-yr experiments, especially in the EucFACE and the AmazonFACE experiments, which are at opposite ends of the moisture index spectrum of these four sites and are particularly susceptible to ENSO (El Niño/Southern Oscillation)-related droughts. To take advantage of unpredictable extreme weather events, it is especially important to have continuous measurements of plant and soil water relations as part of the baseline measurements of these experiments.

Biodiversity

Two immediate questions concerning the link between biodiversity and eCO_2 are: how does eCO_2 alter an ecosystem's biodiversity; and, how does the biodiversity of an ecosystem influence its response to eCO_2? Both of these questions are multi-faceted, and both are resistant to comprehensive answers based on experimental data, even from a 10-yr experiment in a forest ecosystem. While it will be difficult to capture the role of plant diversity or interactions across trophic levels in shaping the response to eCO_2, these experiments can produce useful data on functional plant trait variation that provide insight to link functional diversity and physiological responses to eCO_2 and inform the expression of trait variation in models.

Most Earth system models reduce the tremendous diversity of plant form and function to a small number of plant functional types (PFTs). In these schemes, all of the woody plants, for example, in the AmazonFACE site, including palms, lianas, and trees with a very wide range of wood density, are aggregated to a single PFT: 'broadleaf evergreen tropical tree' in CLM (Oleson *et al.*, 2010) or 'broadleaf evergreen tree' in JULES (Joint UK Land Environment Simulator) (Clark *et al.*, 2011) (which also includes the *Eucalyptus* trees in EucFACE). Simplification is necessary for models that are applied globally, but this construct precludes consideration of species interactions as part of ecosystem response to eCO_2. In addition, since the parameter values of different traits assigned to the PFTs are constants, dynamic responses to eCO_2, for example, changing allocation patterns, are also precluded, and several other plant strategies ignored. New 'trait-enabled' modeling approaches are attempting to incorporate greater variation in the expression of traits within PFTs or abandoning PFTs altogether and characterizing ecosystems as a complex of morphological and physiological traits for which trade-offs between related traits have to be taken into account (e.g. specific leaf area vs leaf longevity and maximum carboxylation rate of Rubisco per leaf area vs leaf nitrogen content, both influencing photosynthetic capacity; see Scheiter *et al.*, 2013; Pavlick *et al.*, 2013; Fyllas *et al.*, 2014; Sakschewski *et al.*, 2015). These modeling approaches require the determination of the range of values for these selected traits; the existence of functional trait databases such as TRY (Kattge *et al.*, 2011) is making this task increasingly feasible. The new generation of FACE experiments can contribute to the model–data interaction needed for advancing the incorporation of functional traits into models. For example, in the two sites with multiple tree species (AmazonFACE and BIFoR-FACE), are there differences in physiological and growth responses among species that can be explained by their trait profile? Models differ widely in how they represent photosynthetic traits of different PFTs, and data for parameterization is notably sparse for tropical PFTs (Rogers, 2014). Across all four experiments, root traits associated with nutrient uptake, including root depth distribution, root tissue density, enzymatic activity (e.g. phosphatase), and mycorrhizal status, and their response to eCO_2, should be analyzed because these root traits link to C, water, and nutrient cycles and are currently missing from models. Agreement on standard protocols to use across all experiments will greatly aid comparisons and development of global databases for model input.

Although the full potential of this new generation of trait-enabled models has yet to be unveiled, their potential to capture more subtle responses of vegetation to eCO_2 make them worth pursuing with this new set of experiments. Additionally, the parameter flexibility this type of model can exhibit is in line with the argument that a no-analogue future climate can originate no-analogue vegetation types around the globe (Reu *et al.*, 2014). Hence, this is an approach that is relevant for data–model integration in the context of FACE experiments that attempt to emulate future environmental conditions.

Research agenda for the next few years

The cross-site science questions proposed here provide a framework for collaborative work across these independent experiments, and they increase the importance of establishing common data formats. Past experience with the first generation of forest FACE experiments has emphasized the importance of establishing this framework early in the development of the experiments, and lessons learned during the process of the FACE-MDS identified the steps needed for robust model–experiment synthesis (Walker *et al.*, 2014). Specific activities that will be pursued include:

- Establish a comprehensive list of data requirements, including recent and current, continuous half-hourly meteorological observations (e.g. air temperature, precipitation, wind speed, radiation).
- Establish a list of data needs for model initialization for each site, including: LAI; leaf mass per unit area; N and P concentrations in

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canopy, leaf litter, and roots; soil texture and elemental composition; and site history.

- Establish a modeling protocol that includes common, harmonized environmental driving data, well-defined instructions for running the model, key vegetation parameters and initialization data, and a common output protocol with built-in redundancy.
- Run a suite of models for each site to establish baseline outputs, identify potential modeling challenges and data needs, and generate hypotheses that can help to structure science questions and cross-site analyses.
- Compare simulations and revisit the protocol to resolve out any problems, standardize across all the models any improvised solutions to modeling problems, and perform quality assurance of input data and consistency of model output.

Since FACE experiments generate a comprehensive suite of data on many ecosystem properties and responses, they create a great opportunity to develop, test, and deploy new and advanced approaches for measuring critical ecosystem responses. For example,

- Tower-based solar-induced fluorescence for documenting responses of gross primary production (GPP) independent of biomass focused measurements of NPP (Damm *et al.*, 2010; Yang *et al.*, 2015). Carbon use efficiency (NPP/GPP) is an important, integrative measure of how forest ecosystems will respond to global anthropogenic change (Malhi *et al.*, 2015), and the new FACE experiments will provide the infrastructure and measurements to test the emerging SIF technology.
- Exploration of the use of spectroscopic and regression-based approaches with the potential to estimate traits such as $V_{c,max}$, foliar N and P, and defense compounds (Asner *et al.*, 2015).
- Ground-based LiDAR to provide detailed description of woody volume, biomass and crown architecture (Calders *et al.*, 2015). This technology promises to revolutionize biomass estimation and enable appropriate scaling of physiological processes using detailed structural data.
- Modeling approaches to tracking ^{13}C movement through plant and soil that exploit the opportunities afforded by the unique ^{13}C signature in the CO_2 sources used to enrich the forests. This approach could be valuable for analyzing critical issues of C allocation and residence times as long as the atmospheric ^{13}C signature of the atmosphere in eCO_2 plots is consistent and well characterized.
- Improved minirhizotrons for root observations that can support more widespread deployment, more rapid image analysis, and increased image resolution including analysis of hyphal production and turnover.
- A coordinated measurement protocol that supports P modeling, including phosphatase activity, N–P interactions, organic P dynamics, P mineralization, sequential P fractionation, rhizosphere enzymes and P solubilization, soil redox, and microbial biomass C, N, and P.

Conclusions

The first generation of forest ecosystem FACE experiments was very successful in generating understanding of how temperate forests respond to a step increase in CO_2 concentration, and providing new insights into the responses of forests to the ongoing increase in atmospheric CO_2. They revealed the importance of C allocation, nutrient interactions, and plant community structure, as well as time and stand development, in determining the fate of C in ecosystems in an atmosphere enriched in CO_2 (Norby & Zak, 2011). The experiments also produced a large volume of new data that were valuable for modeling, and they have pointed the way toward improving the model–data connection (e.g. Medlyn *et al.*, 2015). Although the first FACE experiments were limited to young and relatively homogeneous forest stands, they nevertheless provided a foundation for an exploration of the assumptions embedded in various ecosystem and Earth system models, which should be valuable guidance and increased understanding in the uncertainties inherent in the model predictions of future C fluxes. The model–data interaction was challenging to accomplish in part because it was not initiated until near the conclusions of the experiments, but also because of the inherent disjunct between the transient effects of processes in the ecosystem and longer-term processes in the model for which there may be little site-specific knowledge. With a new generation of FACE experiments being initiated in mature forests over a wide range of climate space and associated biome, we now have a unique opportunity to include the model–data interaction as an integral part of experimental design. Not only will this accelerate the progress and improve the quality of the interaction, but it provides the foundation for developing a set of science questions that will benefit from cross-site comparisons and a collaborative spirit among researchers at otherwise independent experiments.

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