Tansley insight

Forest productivity response to elevated CO_2 in free-air CO_2 enrichment experiments: the 23 percent solution, revisited

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Summary

A synthesis of free-air CO_2 enrichment (FACE) experiments describing the response of forest net primary productivity (NPP) to elevated atmospheric CO_2 published in 2005 has provided a valuable benchmark for ecosystem models used to address the impact of future atmospheric CO_2 levels on forest productivity and the feedback to the atmosphere and climate change. However, that analysis was limited to young, temperate zone tree plantations, and its applicability to other biomes can be questioned. Now, after 20 years, this new analysis includes two sites in much older, mature forests and expanded and updated analyses from the original sites. The original conclusion from 2005 remains valid with only a minor modification. After normalizing to a common CO_2 enrichment of 41%, NPP increased 21.8% in elevated CO_2 across a wide range of forest productivity. The response declined with increasing mean annual temperature, but did not decline with forest age as expected. The response of wood production (18.2%) was somewhat less than that of NPP, but there was no evidence of a CO_2 effect on carbon allocation between long- and short-term carbon pools. This analysis should inform and generate testable hypotheses for new FACE experiments such as the AmazonFACE experiment in a tropical forest.

I. Historical perspective

Charles David Keeling published the first record of the atmospheric CO_2 concentration at the Mauna Loa Observatory in 1960 (Keeling, 1960). Although there were just 2 years of data, the seasonal cycle was readily apparent, and with keen understanding, Keeling interpreted this as indicative of the metabolism of the northern hemisphere biosphere. As the Mauna Loa record was further elaborated and brought to wider attention of the scientific community (Ekdahl & Keeling, 1973), the compelling issues of

impending climate change came to the forefront. An analysis of 'Critical Environmental Problems' in July 1970 (Williamstown, 1970) presciently concluded that the long-term (i.e. beyond 2000) potential consequences of direct climate change resulting from CO_2 'are so large that much more must be learned about future trends of climate change if society is to have time to adjust to changes which may be necessary'. Among their research recommendations were studies of changes in the mass of living matter and the partitioning of CO_2 between the atmosphere, oceans, and biomass. Bacastow & Keeling (1973) introduced the 'biota growth factor' (β) as an adjustable parameter that reflects the degree of stimulation of vegetation productivity, or CO_2 fertilization, needed to balance their geochemical model of the interaction of atmospheric CO_2 with the oceans and land biota. Their model assumed that the land biota responds to gaseous CO_2 approximately as do individual plants grown in glasshouses with adequate light, water, and nutrients, but they recognized that this assumption was unrealistic, and plant growth would not be able to keep pace with fossil fuel consumption. A much better understanding of the interactions between the global carbon cycle, atmospheric CO_2, and climate change was needed. Analyses in the 1970s recognized the potential effect of enhanced photosynthetic production as atmospheric CO_2 concentration increased, but its importance in the carbon cycle was considered to be unclear (Baes *et al.*, 1977) and unlikely to compensate for the CO_2 source from deforestation because of nutrient limitation (Bolin, 1977).

Most of the data on plant responses to atmospheric CO_2 concentration at this time came from short-term studies primarily of crop plants in glasshouses. Kramer (1981) questioned the relevance of these studies to the global carbon cycle: 'In nature, the rate of photosynthesis and biomass production probably is limited more often by water and nitrogen deficiency than by the low CO_2 concentration of the air. Increasing the CO_2 concentration will have little effect if the stomata already are closed, the cell enlargement is inhibited by water stress or the use of photosynthate is limited by lack of nitrogen'. He recognized that forest responses are particularly important globally, and assessments of the role of forests in stabilizing the global CO_2 concentration would require a large research program. Ten years later, Mooney *et al.* (1991) called for elevated CO_2 experiments to be 'undertaken in each of the world's six major biomes (tundra, boreal forest, temperate forest, tropical forest, grassland, and desert)'. By the end of the decade, free-air CO_2 enrichment (FACE) experiments were underway in four temperate forest ecosystems.

II. 2005 analysis of forest NPP response

Forest FACE experiments included two in established forests – DukeFACE, a *Pinus taeda* (loblolly pine) stand in North Carolina (Palmroth *et al.*, 2024), and ORNL-FACE, a *Liquidambar styraciflua* (sweetgum) plantation in Tennessee (Norby *et al.*, 2010) – and two in young, developing tree plantations – RhinelanderFACE, with *Populus, Betula*, and *Acer* trees in Wisconsin (Talhelm *et al.*, 2014), and POP/EuroFACE, with *Populus* clones in Italy (Calfapietra *et al.*, 2003). A prominent objective of these experiments was to provide process-level

information and ecosystem responses for improving and evaluating ecosystem models used in global change analysis. Synthesis papers on soil nitrogen cycling (Zak *et al.*, 2003), soil respiration (King *et al.*, 2004), nitrogen uptake (Finzi *et al.*, 2007), and net primary productivity (NPP) (Norby *et al.*, 2005) were prepared. The objective was to supply experimental evidence that would help to constrain models that include a feedback between terrestrial biosphere metabolism and atmospheric [CO_2]. The synthesis project showed that the response of temperate forest NPP to elevated [CO_2] (eCO_2) was highly conserved across a broad range of productivity, with a stimulation at the median of $23 \pm 2\%$. The surprising consistency of response across diverse sites supported the use of the results as a benchmark to evaluate predictions of ecosystem and global models, while also emphasizing the importance of unresolved questions about carbon partitioning and retention and spatial variation in NPP response caused by availability of other growth-limiting resources. This 2005 synthesis paper, sometimes informally called the '23% paper', has indeed provided an evaluation tool for models (Box 1).

III. A reanalysis of NPP response

Given the importance of the experimental 23% stimulation of NPP as a model benchmark, it is reasonable to question whether this 20-year-old result is still valid. Since the publication of that result, there have been two additional 'second-generation' forest FACE experiments (Norby *et al.*, 2016): EucFACE and BIFoR-FACE (Table 1). The EucFACE experiment in a *Eucalyptus tereticornis* forest in Australia (Jiang *et al.*, 2020) had a negligible NPP response to eCO_2. NPP in the BIFoR-FACE experiment in an old *Quercus robur* woodland in central England increased 10%, considerably less than the previously reported median response of 23% (Norby *et al.*, 2024). Additional years of NPP data also became available for DukeFACE, RhinelanderFACE, and ORNL-FACE in which the NPP response declined in the years after publication of the synthesis report (Norby *et al.*, 2010), and all estimates at DukeFACE and RhinelanderFACE were revised because of improved allometric equations (Talhelm *et al.*, 2014; Palmroth *et al.*, 2024). The response to eCO_2 across these six sites, averaged over years of study, varied from 9.9% to 37.8% (Supporting Information Table S1). Some of this variation in response can be attributed to differences among the experiments in the percentage increase in the CO_2 concentration used in the experiments (Table 1). The NPP response to eCO_2 increased with the CO_2 enrichment ($r^2 = 0.70$; $P = 0.037$; Fig. 1), as would be expected. Hence, 70% of the variance in response across experiments can be explained simply by the actual meaning of 'elevated CO_2'.

All sites can be evaluated on the same basis by using the regression in Fig. 1 to adjust the relative response of NPP to eCO_2 to the average percentage enrichment of all sites (41%) (Box 2). Most previous analyses relied on a simple binary treatment – ambient vs elevated CO_2 without regard to the actual concentration that the experimental trees were exposed. Regressing adjusted NPP in eCO_2 against NPP in aCO_2 (Fig. 2a), and forcing the regression through the origin, yields a slope of 1.218 ± 0.011, corresponding to a 21.8% increase in NPP. This value of 21.8% can be considered the

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Box 1. Model–Data interaction

The 2005 net primary productivity (NPP) synthesis has provided input to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Ciais *et al.*, 2014), model validation of the terrestrial biogeochemistry component of the Earth system models used in the Coupled Model Intercomparison Project (Spafford & MacDougall, 2021), and a benchmark for ecosystem models. Hickler *et al.* (2008) presented model results of NPP response of forests to eCO_2 (550 ppm) and compared the responses with the experimental results. NPP stimulation by eCO_2 in temperate forests (25.7%) and globally (24.5%) compared well with the experimental results, providing confidence in the model projections. They noted that the response was less in boreal forests (15.1%) and greater in tropical forests (35.1%), primarily related to interactions between CO_2 and temperature on photosynthesis (nutrient interactions were not included in this version of LPJ-GUESS). Similarly, Matthews (2007), using the University of Victoria Earth System Climate Model, simulated the response to a step change in CO_2 of a temperate forest and reported a 24.6% increase in NPP; the similarity to forest free-air CO_2 enrichment (FACE) results was considered especially encouraging with regard to model performance. More recently, Haverd *et al.* (2020) concluded that the observed increase in gross primary production was primarily attributable to rising atmospheric CO_2. Their analysis using the Community Atmosphere-Biosphere Land Exchange model was supported by the consistency of their modeled NPP response to that reported in Norby *et al.* (2005). Similar to the analysis of Hickler *et al.* (2008), a larger response was modeled in tropical forests and a lesser response in boreal forests than in the results from FACE experiments in temperate forests (Fig. B1). However, it is important to note that reproducing the experimental results does not necessarily mean the model is correctly simulating the underlying processes – the model could be 'right' for the wrong reason (Zaehle *et al.*, 2014).
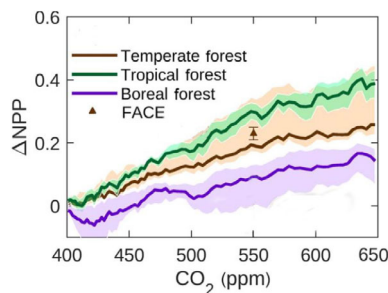

Fig. B1 CO_2 fertilization effect on net primary productivity (NPP). The solid lines represent the median predictions of the Community Atmosphere–Biosphere Land Exchange model, using fixed land use and climate and rising CO_2 following the trajectory of RCP8.5 for each of temperate, tropical, and boreal forests, referenced to a 400-ppm baseline. Shading represents the 25th and 75th percentiles. The data point represents the fractional increase in NPP (0.23 or 23%) from free-air CO_2 enrichment (FACE) experiments in Norby *et al.* (2005). Figure is modified from Haverd *et al.* (2020).

Fig. 1 CO_2 enrichment used in six free-air CO_2 enrichment (FACE) experiments, expressed as the percentage increase in CO_2 concentration relative to ambient concentration, explains a significant amount of variation in response to net primary productivity across sites. The data shown are the mean across years of observation $\pm$ SD. The equation by linear regression is as follows: response $= 1.337 \times \%CO_2$ enrichment $- 31.827$; $r^2 = 0.703$, $P = 0.037$, $F_{1,4} = 9.48$. The intercept, indicating the response with no added CO_2, is not significantly different from 0 ($P = 0.153$, CI: -82.0 to 18.3). The average CO_2 enrichment across these sites was 41% or 158 ppm.

(Table S1). Following the same analytical approach as with NPP, regressing adjusted DMI in eCO_2 against DMI (Fig. 2b) in aCO_2 yields a slope of $1.182 \pm 0.012\%$.

The addition of new FACE experiments has expanded the range of site conditions and forest stand attributes beyond the previous analysis of young, temperate zone sites (Table 1). Climatic factors have been proposed as influencing forest response to eCO_2: temperature (Hickler *et al.*, 2008; Norby *et al.*, 2016) or precipitation (Mooney *et al.*, 1991; Cui *et al.*, 2024). Response of NPP to eCO_2, adjusted to a common CO_2 enrichment of 41%, declined with increasing mean annual temperature (MAT) (Fig. 3a); there was no relationship with mean annual precipitation (Fig. 3b). Response declined with increasing length of growing season (Fig. 3c), which may seem counterintuitive, but length of growing season is closely correlated with MAT, which likely explains this result. Climatic influences on response to eCO_2 are confounded by effects of site fertility. For example, the minimal response at the site with the longest growing season (EucFACE) is more likely related to the low P availability (Jiang *et al.*, 2020), in contrast to the lack of strong nutrient limitation at Rhinelander with the shortest growing season. Soil nutrient status undoubtedly is an important modifier of response to eCO_2, but there is not a simple or consistent metric of nutrient availability that supports a quantitative analysis of its relationship to CO_2 response. There was no relationship with total soil N (Fig. 3d), which is an imperfect indicator of N availability, but N limitation was considered the primary reason for the declining response at ORNL-FACE (Norby *et al.*, 2010) and is an especially important focus of models of eCO_2 responses (Zaehle *et al.*, 2014). Walker *et al.* (2021) noted that despite the increases in biomass production is early-successional stands, there was no increase in late-successional stands, but the current analysis reveals no relationship between response and age of the site when the response is adjusted for the lower CO_2 enrichment used in the late-successional experiments (Fig. 3e). BIFoR-FACE, which is the oldest stand in this analysis, had a larger response than

best estimate from this dataset describing the response to a 41% increase in CO_2 and corresponding to a β of 0.57 using the log–log formulation favored by Walker *et al.* (2021) (Box 2).

More data are available from FACE experiments on aboveground wood production (dry matter increment, DMI) than for NPP, including data from the Bangor FACE experiment (Smith *et al.*, 2013) and additional years of data from BIFoR-FACE
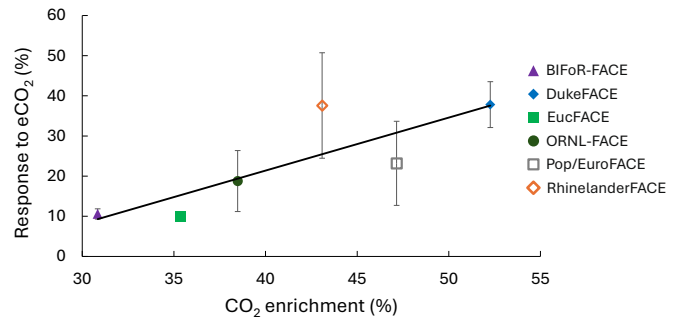

Box 2. Calculation considerations

The calculation of net primary productivity (NPP) in each experiment included the major components – leaf, wood, and fine-root production, and (if present) reproductive output, expressed as g dry matter $m^{-2} yr^{-1}$. Additional minor components of NPP were included in some analyses: exudation at BIFoR-FACE and VOCs at EucFACE. Only data that were published as of March 2025 are included in this analysis. The ongoing experiments (BIFoR-FACE and EucFACE) will be producing additional NPP and tree growth data, and the current estimates for EucFACE will change as a result of new allometry based on a terrestrial laser scan of the trees (Terryn *et al.*, 2024).

Normalization to a common CO_2 exposure regime is made difficult because actual attained CO_2 concentration data from ambient and elevated plots often are not reported as they should be. In addition, the baseline (ambient CO_2) has increased 17% from 364 ppm when the first experiments began to 427 ppm today, and it will continue to change. Hence, the response ratio has been normalized to a constant percentage increase in CO_2. Another approach is to express response in terms of the β-factor. Rewritten from the original formulation by Bacastow & Keeling (1973), Amthor & Koch (1996) defined β as follows

$$\beta = [(NPPe/NPPa) - 1] / \log_e(eCO_2/aCO_2)$$

but Walker *et al.* (2021) concluded a log–log formulation was more robust:

$$\beta = \log_e(NPPe/NPPa) / \log_e(eCO_2/aCO_2)$$

Normalization of the response ratio to a constant absolute difference in eCO_2 and aCO_2 or to $\log_e(eCO_2/aCO_2)$ yielded virtually identical results as normalization based on % increase in CO_2.

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might be expected because N deposition and enhancement of N availability supported a CO_2 fertilization effect (Norby *et al.*, 2024).

IV. Allocation and wood production

While NPP is a key, integrative and ecologically relevant metric of forest response to global change and an important and useful benchmark for ecosystem models (Box 1), it does not directly provide information about carbon sequestration and the potential feedback provided by CO_2 fertilization to the global C cycle. The critical consideration is allocation to the different components of NPP and their respective turnover rates. Production of wood can remove carbon from the atmosphere for decades or centuries and is the focus of forests as part of climate mitigation solutions, whereas leaves and fine-roots turn over rapidly and release most of the carbon allocated to those tissues back to the atmosphere in a year or two. At DukeFACE, there was a shift in allocation toward woody biomass (Palmroth *et al.*, 2024), whereas at ORNL-FACE, an initial increase in woody biomass increment was not maintained, and the increase in NPP was primarily attributed to fine-root production, which nevertheless led to greater soil C (Iversen & Norby, 2008). By contrast, the increase in NPP at BIFoR-FACE was primarily attributed to increased production of stem wood (Norby *et al.*, 2024). Gross primary production increased in eCO_2 at EucFACE, but there was no increase in biomass production, suggesting allocation was instead to exudation

and belowground respiration (Jiang *et al.*, 2020). Tree ring width of 100-yr-old deciduous hardwood trees (Bader *et al.*, 2013) or basal area increment of 110-yr-old *Picea abies* trees (Klein *et al.*, 2016) in webFACE studies in Switzerland showed no response to eCO_2 despite increases in photosynthesis in eCO_2. For the subset of observations in which wood production could be calculated as a fraction of NPP, wood fraction was 0.58 ± 0.02 in aCO_2 and 0.56 ± 0.02 in eCO_2, indicating no effect of eCO_2 on allocation to long-lived tissue.

V. Comparison with other syntheses

The response of NPP to eCO_2 reported here (21.8% increase) is very close to that reported previously (Norby *et al.*, 2005). The lower responses at new sites in late-successional stands (BIFoR-FACE and EucFACE) and the decline in response in ORNL-FACE were offset by higher-than-previous estimates at DukeFACE due to additional years of data and revised allometry. Several recent meta-analyses reported somewhat different values, reflecting very different choices of data. Cui *et al.* (2024) concluded that NPP of forests increases 27% in eCO_2, but the data in the analysis included pretreatment responses and duplicate values from the same experiment reported in different papers. Terrer *et al.* (2016) reported a 30% increase in ectomycorrhizal-dominated forests and 7% in arbuscular mycorrhizal-dominated forests (20% overall), but this analysis included many seedling and sapling studies, which are not representative of the responses of trees in a closed-canopy forest. The dataset used by Wang & Wang (2021) to support their conclusion of a 32% increase in tree biomass production was dominated by seedling and sapling studies. Young trees in open-top chambers undergoing exponential growth, with increasing leaf area supporting progressively increased biomass production, can exhibit very large relative increases in aboveground growth (average of 73%), but when expressed as growth per unit leaf area to be more relevant to tree growth in an established forest with relatively constant leaf area, the response is a fairly constant 26% (Norby *et al.*, 1999). Decade-long aboveground biomass increment in early-successional forest stands – FACE experiments at Duke, ORNL, Rhinelander; and an open-top chamber experiment in Florida (Hungate *et al.*, 2013) – increased 29.1% in eCO_2 (Walker *et al.*, 2019). The lesser response of DMI reported here (18.2%) can be attributed in part to the inclusion of older, more mature stands that were less responsive to eCO_2.

VI. Predictions for future studies

This analysis should be useful for establishing hypotheses to test in future FACE experiments in different biomes. CO_2 treatments in the long-anticipated tropical forest FACE experiment, Amazon-FACE, will begin in 2025 (Lapola *et al.*, 2024). Previous analyses and FACE experiments suggest alternative hypotheses regarding the response of NPP in this highly diverse, wet tropical forest. A conceptual understanding before any FACE experiments suggested that a wet tropical forest would have a small response given the low water stress and high nutrient deficiency (Mooney *et al.*, 1991; Norby *et al.*, 2016). The global modeling of NPP response
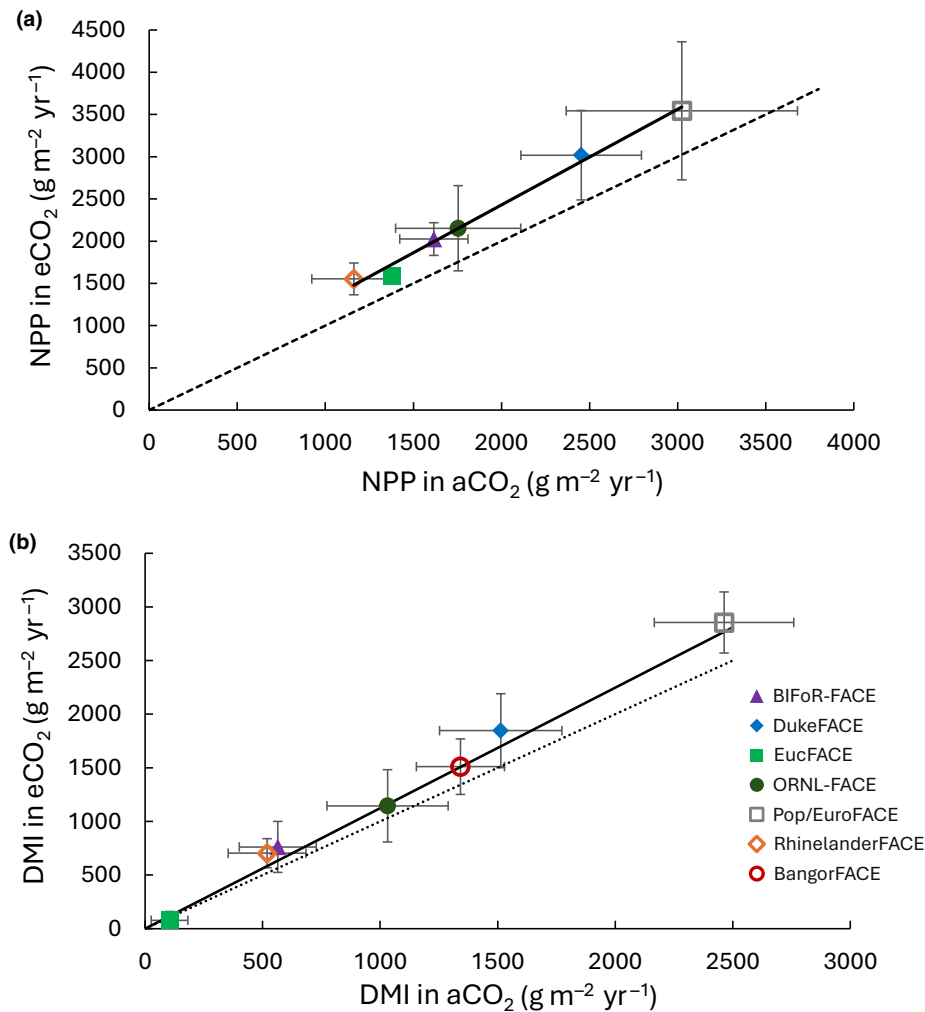
Fig. 2 Forest response to CO_2 enrichment in free-air CO_2 enrichment (FACE) experiments. (a) Net primary productivity (NPP) in eCO_2 (NPPe) vs NPP in aCO_2 (NPPa). The NPPe is adjusted to a common CO_2 enrichment of 41% based on the relationship in Fig. 1. Error bars are SD based on data from each year. The dotted line is the 1 : 1 relationship. The slope of the linear regression equation of NPPe vs NPPa using data from all years at each site (Supporting Information Table S1) is 1.218 ± 0.011 ($F_{1,39} = 11\,608$, $r^2 = 0.997$, $P < 0.001$, CI: 1.197–1.245). (b) Similar analysis with aboveground dry matter increment (DMI) yields a slope of 1.182 ± 0.012 ($F_{1,54} = 9405$, $r^2 = 0.994$, $P < 0.001$, CI: 1.157–1.206).

following the 2005 synthesis indicated that tropical systems would have a larger relative response than the 23% demonstrated in temperate systems because of greater photosynthetic enhancement at higher temperatures (Hickler *et al.*, 2008; Box 1), a conclusion challenged by this current analysis showing a significant decline in response with increasing temperature. Modeling which incorporated nutrient interactions came to a different prediction for AmazonFACE: phosphorus limitation will reduce the response of NPP (Fleischer *et al.*, 2019). Although there was not a significant relationship between stand age and response, the two oldest sites (EucFACE and BIFoR-FACE) did have the smallest response, and the AmazonFACE forest is much older. Taken together, Amazon-FACE is predicted to have a small response to eCO_2, but this prediction needs to be tested, and the intended CO_2 treatment of +200 ppm (47% increase from a baseline of 427 ppm) should help in detecting a response (Fig. 1).

VII. Conclusions

FACE experiments have been invaluable in describing a wide range of physiological and ecological responses (Ainsworth & Long, 2005; Norby & Zak, 2011) and informing ecosystem models (Medlyn *et al.*, 2015). This expanded analysis of forest productivity response to elevated CO_2 in FACE experiments has confirmed the previous analysis, which was limited to early reports from young tree plantations. The average response across sites to a standardized CO_2 enrichment of 41% (or 158 ppm) was 21.8%, only slightly different from the previous report of 23%. The response declined with MAT in contrast to some model predictions. Other possible correlates of response were likely confounded by the moderating effect of site fertility. This analysis should inform and generate testable hypotheses for new FACE experiments such as the AmazonFACE experiment in a tropical forest. Finally, it is noteworthy that this discussion started with the Keeling's analysis of CO_2 fertilization 65 years ago and the first theoretical expression of the biotic growth factor β in 1973 as 0.56. We can now revise that value to 0.57 – a miniscule change, but a large increase in empirical evidence provided by many hundreds of scientists.

Fig. 3 Relationship between net primary productivity (NPP) response to eCO_2, adjusted to a common CO_2 enrichment of 41%, with factors proposed to influence the response. Data points are means across years of observation; SD are shown for relationships with significant linear regressions. (a) Adjusted response to NPP declined with increasing mean annual temperature (MAT). Response $= -1.433 \times MAT + 40.96$; $r^2 = 0.866$, $P = 0.007$, $F_{1,4} = 25.78$. (b) There is no significant relationship between response and mean annual precipitation. (c) Response declined with the length of the growing season: response $= -0.107 \times length + 46.847$; $r^2 = 0.904$, $P = 0.004$, $F_{1,4} = 37.81$. (d) There is no relationship with total soil nitrogen (N) or with (e) stand age.
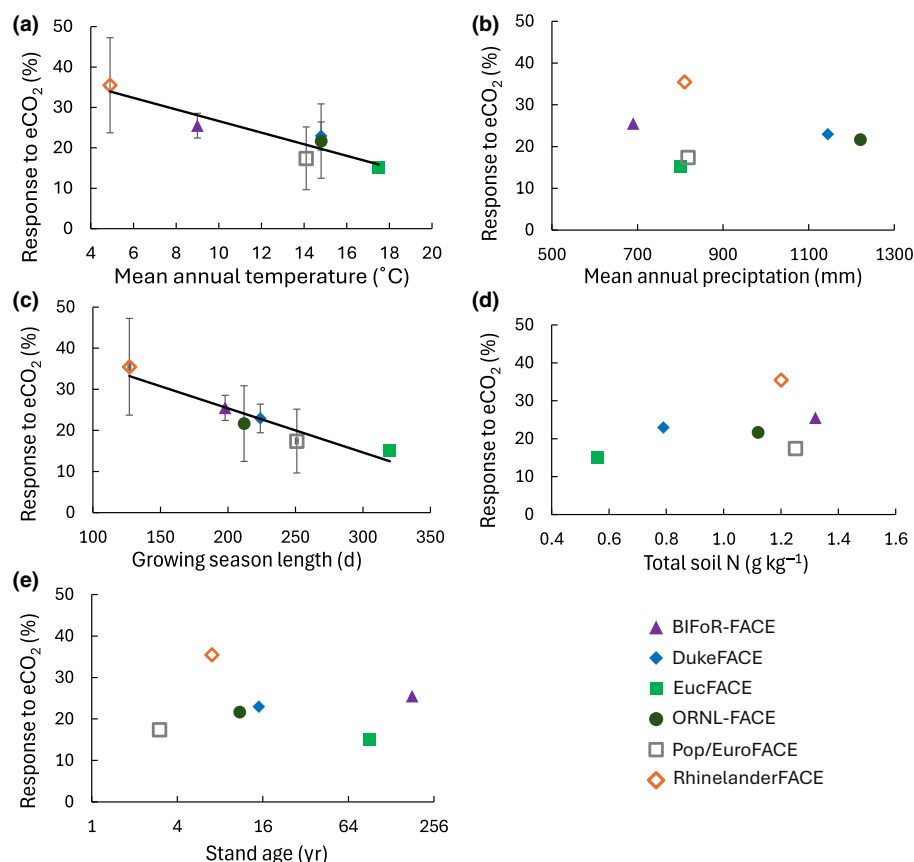
Table 1 Description of free-air CO_2 enrichment (FACE) experiments used in this analysis.

	Location (lat, lon)	Species	Age (yr)	MAT (°C)	MAP (mm)	Total soil nitrogen (g kg^{-1})	Length of growing season (d)	aCO$_2$ (ppm)	eCO$_2$ (ppm)	Reference
BIFoR-FACE	52.801, −2.30	*Quercus robur*	180	9	690	1.32	198	428	560	Norby *et al.* (2024)
DukeFACE	35.97, −79.09	*Pinus taeda*	15	14.8	1145	0.79	224	375	571	Palmroth *et al.* (2024)
EucFACE	−33.36, 150.44	*Eucalyptus tereticornis*	90	17.5	800	0.56	320	390	528	Jiang *et al.* (2020)
ORNL-FACE	35.90, −84.34	*Liquidambar styraciflua*	11	14.8	1221	1.12	212	395	547	Norby *et al.* (2010)
Pop/EuroFACE	42.22, 11.48	*Populus alba, P. nigra, P × euramericana*	3	14.1	818	1.25	251	369	543	Calfapietra *et al.* (2003); Liberloo *et al.* (2006)
RhinelanderFACE	45.68, −89.65	*P. tremuloides, Betula papyrifera*	7	4.9	810	1.20	127	369	528	Talhelm *et al.* (2014)
BangorFACE	53.02, −4.02	*Alnus glutinosa, Betula pendula*	1	11.5	1034	2.60	262	380	580	Smith *et al.* (2013)

Species listed are the dominant species of the site and the source of analysis of dry matter increment. Net primary productivity was measured at the plot level, including understory species. Lat/lon, latitude and longitude of the site; MAP, mean annual precipitation; MAT, mean annual temperature; age is the stand age at the beginning of the experiment. Growing season is defined as the longest continuous period of nonfreezing temperatures; data from https://weatherspark.com/. CO_2 concentrations in the ambient (aCO_2) and elevated (eCO_2) experimental plots are the values used in the calculations in this paper, but accurate experimental concentrations are often difficult to extract from the literature. Data sources are given in Supporting Information Table S1.

Competing interests

None declared.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Data on net primary productivity and dry matter increment extracted from primary sources and used in the analyses in Figs 1–3.

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