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Review

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Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO_2

Author for correspondence:
Anthony P. Walker
Email: walkerap@ornl.gov

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Anthony P. Walker[1], Martin G. De Kauwe[2,3,4], Ana Bastos[5], Soumaya Belmecheri[6], Katerina Georgiou[7], Ralph F. Keeling[8], Sean M. McMahon[9], Belinda E. Medlyn[10], David J. P. Moore[11], Richard J. Norby[1], Sönke Zaehle[12], Kristina J. Anderson-Teixeira[13,14], Giovanna Battipaglia[15], Roel J. W. Brienen[16], Kristine G. Cabugao[1], Maxime Cailleret[17,18], Elliott Campbell[19], Josep G. Canadell[20], Philippe Ciais[21], Matthew E. Craig[1], David S. Ellsworth[10], Graham D. Farquhar[22], Simone Fatichi[23,24], Joshua B. Fisher[25], David C. Frank[6], Heather Graven[26], Lianhong Gu[1], Vanessa Haverd[20], Kelly Heilman[6], Martin Heimann[12], Bruce A. Hungate[27], Colleen M. Iversen[1], Fortunat Joos[28], Mingkai Jiang[10], Trevor F. Keenan[29,30], Jürgen Knauer[20], Christian Körner[31], Victor O. Leshyk[27], Sebastian Leuzinger[32], Yao Liu[1], Natasha MacBean[33], Yadvinder Malhi[34], Tim R. McVicar[35,36], Josep Penuelas[37,38], Julia Pongratz[39,40], A. Shafer Powell[1], Terhi Riutta[34], Manon E. B. Sabot[2,3,4], Juergen Schleucher[41], Stephen Sitch[42], William K. Smith[11], Benjamin Sulman[1], Benton Taylor[9], César Terrer[43], Margaret S. Torn[30], Kathleen K. Treseder[44], Anna T. Trugman[45], Susan E. Trumbore[12], Phillip J. van Mantgem[46], Steve L. Voelker[47], Mary E. Whelan[48] and Pieter A. Zuidema[49]

[1]Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA; [2]ARC Centre of Excellence for Climate Extremes, University of New South Wales, Sydney, NSW 2052, Australia; [3]Climate Change Research Centre, University of New South Wales, Sydney, NSW 2052, Australia; [4]Evolution and Ecology Research Centre, University of New South Wales, Sydney, NSW 2052, Australia; [5]Ludwig Maximilians University of Munich, Luisenstr. 37, Munich 80333, Germany; [6]Laboratory of Tree Ring Research, University of Arizona, 1215 E Lowell St, Tucson, AZ 85721, USA; [7]Department of Earth System Science, Stanford University, Stanford, CA 94305, USA; [8]Scripps Institution of Oceanography, UC San Diego, La Jolla, CA 92093, USA; [9]Smithsonian Environmental Research Center, Edgewater, MD 21037, USA; [10]Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2751, Australia; [11]School of Natural Resources and the Environment, 1064 East Lowell Street, Tucson, AZ 85721, USA; [12]Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, Jena 07745, Germany; [13]Conservation Ecology Center, Smithsonian Conservation Biology Institute, MRC 5535, Front Royal, VA 22630, USA; [14]Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Panama City, Panama; [15]Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, Università della Campania, Caserta 81100, Italy; [16]School of Geography, University of Leeds, Leeds, LS6 9JT, UK; [17]INRAE, UMR RECOVER, Aix-Marseille Université, 3275 route de Cézanne, Aix-en-Provence Cedex 5 13182, France; [18]Swiss Federal Institute for Forest Snow and Landscape Research (WSL), Zürcherstrasse 111, 8903 Birmensdorf, Switzerland; [19]Department of Geography, University of California Santa Barbara, Santa Barbara, CA 93106, USA; [20]CSIRO Oceans and Atmosphere, GPO Box 1700, Canberra, ACT 2601, Australia; [21]Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-UVSQ, Université Paris-Saclay, Gif-sur-Yvette F-91191, France; [22]Plant Sciences, Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia; [23]Department of Civil and Environmental Engineering, National University of Singapore, 1 Engineering Drive 2, Singapore 117576, Singapore; [24]Institute of Environmental Engineering, ETH Zurich, Stefano-Franscini Platz 5, Zurich 8093, Switzerland

[25]Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Dr., Pasadena, CA 91109, USA; [26]Department of Physics, Imperial College London, South Kensington Campus, London, SW7 2AZ, UK; [27]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA; [28]Climate and Environmental Physics, Physics Institute and Oeschger Centre for Climate Change Research, University of Bern, Sidlerstr. 5, Bern CH-3012, Switzerland; [29]Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA 94720, USA; [30]Earth and Environmental Sciences Area, Lawrence Berkeley National Lab., Berkeley, CA 94720, USA; [31]Department of Environmental Sciences, Botany, University of Basel, Basel 4056, Switzerland; [32]School of Science, Auckland University of Technology, Auckland 1142, New Zealand; [33]Department of Geography, Indiana University, Bloomington, IN 47405, USA; [34]School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, UK; [35]CSIRO Land and Water, GPO Box 1700, Canberra, ACT 2601, Australia; [36]Australian Research Council Centre of Excellence for Climate Extremes, 142 Mills Rd, Australian National University, Canberra, ACT 2601, Australia; [37]CSIC, Global Ecology CREAF-CSIC-UAB, Bellaterra, Barcelona, Catalonia 08193, Spain; [38]CREAF, Cerdanyola del Vallès, Barcelona, Catalonia 08193, Spain; [39]Ludwig Maximilians University of Munich, Luisenstr. 37, Munich 80333, Germany; [40]Max Planck Institute for Meteorology, Bundesstr. 53, 20146 Hamburg, Germany; [41]Department of Medical Biochemistry & Biophysics, Umeå University, Umea 901 87, Sweden; [42]College of Life and Environmental Sciences, University of Exeter, Exeter Laver Building, EX4 4QF, UK; [43]Physical and Life Sciences Directorate, Lawrence Livermore National Laboratory, Livermore, CA 94550, USA; [44]Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA 92697, USA; [45]Department of Geography, 1832 Ellison Hall, Santa Barbara, CA 93016, USA; [46]U.S. Geological Survey, Western Ecological Research Center, Arcata, CA 95521, USA; [47]Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA; [48]Department of Environmental Sciences, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA; [49]Forest Ecology and Forest Management group, Wageningen University, PO Box 47, Wageningen 6700 AA, the Netherlands

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Summary

Atmospheric carbon dioxide concentration ([CO_2]) is increasing, which increases leaf-scale photosynthesis and intrinsic water-use efficiency. These direct responses have the potential to increase plant growth, vegetation biomass, and soil organic matter; transferring carbon from the atmosphere into terrestrial ecosystems (a carbon sink). A substantial global terrestrial carbon sink would slow the rate of [CO_2] increase and thus climate change. However, ecosystem CO_2 responses are complex or confounded by concurrent changes in multiple agents of global change and evidence for a [CO_2]-driven terrestrial carbon sink can appear contradictory. Here we synthesize theory and broad, multidisciplinary evidence for the effects of increasing [CO_2] (iCO_2) on the global terrestrial carbon sink. Evidence suggests a substantial increase in global photosynthesis since pre-industrial times. Established theory, supported by experiments, indicates that iCO_2 is likely responsible for about half of the increase. Global carbon budgeting, atmospheric data, and forest inventories indicate a historical carbon sink, and these apparent iCO_2 responses are high in comparison to experiments and predictions from theory. Plant mortality and soil carbon iCO_2 responses are highly uncertain. In conclusion, a range of evidence supports a positive terrestrial carbon sink in response to iCO_2, albeit with uncertain magnitude and strong suggestion of a role for additional agents of global change.

I. Introduction

Photosynthesis uses the energy in sunlight to bind CO_2 to a five-carbon sugar, transferring CO_2 from the atmosphere to plants (Calvin & Benson, 1948; Farquhar *et al.*, 1980). Sugars produced by photosynthesis provide the building blocks and the primary fuel for much of life on Earth. Plant tissues, many microbes, animals, and dead organic matter are all composed of carbon-rich compounds formed from these photosynthetic sugars. In many environments, an increase in atmospheric CO_2 concentration $[CO_2]$ increases photosynthesis. Thus an increase in $[CO_2]$ leads to greater plant sugar availability with the potential to increase the total amount of carbon stored in the live and dead organic matter in an ecosystem. These observations have led to the CO_2-fertilization hypothesis (Box 1): that plant responses to increasing atmospheric $[CO_2]$ drive increases in terrestrial-ecosystem carbon storage, creating negative feedback on atmospheric $[CO_2]$ growth.

Since the industrial revolution, human activities have increased $[CO_2]$ by 48% (1760–2019, 277–411 ppm), an increase in atmospheric CO_2-carbon of 277 Pg C (Friedlingstein *et al.*, 2019). However, global-scale carbon accounting quantifies anthropogenic emissions to the atmosphere at 645 Pg C and suggests a substantial 'natural' terrestrial carbon sink (a net flux of carbon from the atmosphere to intact terrestrial ecosystems) which currently removes the equivalent of 33 $\pm$ 9% of anthropogenic atmospheric CO_2 (2009–2018; Friedlingstein *et al.*, 2019). Along with the ocean carbon sink, this terrestrial carbon sink is mitigating the rate of climate change. Process-based carbon-cycle models attribute increasing $[CO_2]$ (iCO_2; Table 1) as the primary driver of the terrestrial carbon sink, albeit with substantial uncertainty (Huntzinger *et al.*, 2017; Arora *et al.*, 2019). However, iCO_2 is not the only global-change factor that can influence terrestrial carbon stocks. Anthropogenic land-use and land-cover change (hereafter land-use change) and recovery (Pugh *et al.*, 2019), nitrogen cycle changes (Fowler *et al.*, 2013), and climate change all affect ecosystem carbon stocks (Keenan & Williams, 2018). A vast and overwhelming literature often disagrees about the size and duration of CO_2-driven increases in terrestrial carbon storage and predictive understanding of this process is a long-standing and unresolved scientific goal.

Predictive understanding of how terrestrial ecosystems respond to iCO_2 requires knowledge of a range of processes, their interactions, and how these processes scale. For example, terrestrial ecosystem responses begin with photosynthesis inside the leaf, yet scale to have long-term global impacts. All the relevant processes must be understood across scales, and ultimately at the global scale because iCO_2 and climate change are global-scale phenomena with decadal to centennial dynamics.

Given that *c.* 50% of plant biomass is carbon-acquired via photosynthesis, it is reasonable to assume that increased photosynthesis increases plant biomass production (BP) and experimentally elevated $[CO_2]$ (eCO_2) commonly increases BP (e.g. Baig *et al.*, 2015). However, in natural ecosystems iCO_2 may not always increase BP, primarily because plant tissues require nutrients, and BP responses to iCO_2 will interact with soil nutrient availability and other limiting factors (Strain & Bazzaz, 1983; Rastetter *et al.*, 1997). A related argument is that present-day $[CO_2]$ is likely to supply plants with unprecedented carbon availability that may be surplus to BP requirements (Körner, 2003a). This is because for at least one million years before the industrial revolution $[CO_2]$ was much lower (170–300 ppm) (Bereiter *et al.*, 2015).

Table 1 Acronyms and abbreviations.

A_{net}	Net photosynthetic carbon assimilation
fAPAR	Fraction absorbed photosynthetically active radiation
BAI	Basal area increment
BP	Biomass production, the sum of all tissue production over a given time, typically 1 yr
C_x	Carbon in pool *x*, where *x* is either vegetation ('veg'), soil, ecosystem ('eco')
CO_2	Carbon dioxide
$[CO_2]$	Atmospheric CO_2 concentration
eCO_2	Elevated CO_2 from experiments and CO_2 springs
FACE	Free-air CO_2 enrichment
GPP	Gross primary production
g_s	Stomatal conductance
iCO_2	Increasing CO_2 from fossil fuel emissions and land-use change
iWUE	Intrinsic WUE (A_{net}/g_s)
k_x	Turnover rate of carbon in pool *x* (see C_x)
LAI	Leaf area index
NBP	Net biome production, net land atmosphere exchange
NEP	Net ecosystem production
OCS	Carbonyl sulphide
UE	Use efficiency
VPD	Vapour pressure deficit
WUE	Water-use efficiency (transpiration/BP)

Ecosystem carbon stocks are the result of both inputs (BP for plants or litter production for soils) and outputs. Thus for the CO_2-fertilization hypothesis to hold true, the residence time of carbon in an ecosystem must not be reduced by an amount that would negate effects of increased BP on terrestrial carbon pools. However, it has been suggested that both vegetation and soil carbon residence times may be reduced by iCO_2 (van Groenigen *et al.*, 2014; Körner, 2017).

Drawing from multiple disciplines, vast quantities of diverse data have been collected on the $[CO_2]$ responses of many processes. Often this evidence can appear conflicting. For example, many free-air CO_2 enrichment (FACE) experiments show BP gains (Walker *et al.*, 2019), while others show none (Bader *et al.*, 2013; Ellsworth *et al.*, 2017). Many tree-ring studies indicate historical increases in intrinsic water-use efficiency (iWUE) but no detectable change in BP (Peñuelas *et al.*, 2011; van der Sleen *et al.*, 2015), while the majority of forest-inventory analyses suggest biomass gains (Brienen *et al.*, 2015; Hubau *et al.*, 2020). Flux-tower data, global CO_2-flask networks, and remote-sensing data are now of sufficient timescales (decades) to study CO_2 responses against background variability, but have led to different inferences (Kolby Smith *et al.*, 2016; Fernández-Martínez *et al.*, 2017).

This literature represents a wealth of information and inference that can appear fragmented, posing an opportunity for integration. Thus our overall goal is to provide a synthetic review of key lines of evidence related to the CO_2-fertilization hypothesis, specifically:
(**1**) overview of theory and potential mechanisms within the CO_2-fertilization hypothesis;

Box 1 The CO_2-fertilization hypothesis.

The stimulation of photosynthesis by CO_2 has been called 'CO_2 fertilization' (Ciais *et al*., 2014), a term that goes back to global carbon cycle modelling in the 1970s (Bacastow & Keeling, 1973). However, 'CO_2 fertilization' or the 'CO_2-fertilization effect' have been used to refer to the [CO_2] response of any number of variables across scales. This broad usage has been a source of confusion and, more commonly, 'fertilization' is a value-laden, agricultural term that means the addition of nutrients to increase crop yield. Acknowledging the precedence of the term, its multiple uses, and the fact that CO_2 responses of some processes may be neutral or negative, we opt to refer to 'CO_2 responses' of explicitly defined variables and scales.

We reserve the term 'CO_2 fertilization' solely to label the hypothesis that: plant responses to increasing atmospheric [CO_2] lead to increasing terrestrial-ecosystem carbon storage, causing negative feedback on atmospheric [CO_2] growth. This definition of the CO_2-fertilization hypothesis is explicit about the feedback on atmospheric [CO_2] growth, implying the potential of this process to slow climate change. The hypothesis is therefore defined at climate-change relevant scales, that is, global in space and decadal to centennial in time.

For the CO_2-fertilization hypothesis to be true, Eqn B1 must be positive at the global scale and over a specified time period:

$$\Delta \mathrm{NEP} = \Delta \mathrm{C}_{\mathrm{eco}} = \Delta \mathrm{C}_{\mathrm{veg}} + \Delta \mathrm{C}_{\mathrm{soil}} \qquad \text{Eqn B1}$$

where NEP is net ecosystem production, C_{veg} and C_{soil} are plant and soil (including litter and coarse woody debris) terrestrial carbon that sum to give total ecosystem carbon (C_{eco}), and Δ represents change as a result of increasing [CO_2]. A change in carbon storage is the net result of inputs and outputs (Olson, 1963):

$$\mathrm{dC}/\mathrm{d}t = I - k\mathrm{C} \qquad \text{Eqn B2}$$

where C is stored carbon, I is the input, and k is the turnover rate of the pool (the inverse of mean residence time).

Net primary production (NPP) represents the net input of carbon to C_{veg} and is calculated as gross primary production (GPP), which responds directly to iCO_2, minus autotrophic respiration (R_a). In practice, NPP is often estimated from total biomass production (BP), the sum of leaf, wood, root, and reproductive tissue production over a given time period (Vicca *et al*., 2012). In addition to BP, NPP includes carbon used for the production of volatiles, root exudation, supply to symbionts, and changes in nonstructural carbohydrates (NSCs). However, these carbon fluxes are difficult to measure and often have very short residence times, somewhat akin to respiratory carbon. Therefore, to align with measurements and residence time we use BP to decompose changes in C_{veg}:

$$\mathrm{dC}_{\mathrm{veg}}/\mathrm{d}t = \mathrm{BP} - k_{\mathrm{veg}}\mathrm{C}_{\mathrm{veg}} \qquad \text{Eqn B3}$$

where k_{veg} is the turnover (litterfall and mortality) rate of vegetation biomass. For soils, the inputs to C_{soil} are vegetation litter production and mortality, as well as nonbiomass NPP fluxes (S) that include exudation and carbon supply to symbionts:

$$\mathrm{dC}_{\mathrm{soil}}/\mathrm{d}t = k_{\mathrm{veg}}\mathrm{C}_{\mathrm{veg}} + S - k_{\mathrm{soil}}\mathrm{C}_{\mathrm{soil}} \qquad \text{Eqn B4}$$

where k_{soil} represents the turnover rate of soil carbon caused by microbial decomposition.

(**2**) quantitative evaluation of the evidence, identifying agreement and major conflicts;
(**3**) resolution of apparent conflicts and, where this is not possible, identification of key knowledge gaps to guide future studies.

We structure this multidisciplinary review within the mechanistic theory of the five broad processes that are key to the CO_2-fertilization hypothesis (Box 1; Fig. 1a): gross primary production (GPP), plant BP, vegetation mortality rate (k_{veg}), soil organic matter (SOM) decomposition rate (k_{soil}), and terrestrial carbon storage (C_{eco}). Within each of these high-level processes, numerous interrelated mechanisms and subprocesses shape terrestrial ecosystem CO_2 responses (Fig. 1b; Section II).

Within these processes we integrate four primary evidence themes (Box 2). eCO_2 studies in Evidence theme 1 provide the only direct evidence for CO_2 responses but are restricted in space and time. Observation studies (Evidence themes 2–4) span a broader range of evidence types covering larger spatial scales and longer temporal scales but provide only indirect evidence for the effect of iCO_2 on terrestrial ecosystems.

To quantify and standardize CO_2 effects across variables and varying ranges of [CO_2] we report data as a relativized β-factor:

$$\beta = \log_e\left(y_e/y_a\right)/\log_e\left(\mathrm{CO}_{2,e}/\mathrm{CO}_{2,a}\right) \qquad \text{Eqn 1}$$

where y_a and y_e are the values of any response variable at lower [CO_2] ($CO_{2,a}$) and higher [CO_2] ($CO_{2,e}$), respectively. Other methods to calculate the β-factor have been proposed (e.g. Friedlingstein *et al.*, 1995) but we use Eqn 1 for the ease of interpretation that results from scale independence (Supporting Information Notes S1; Fig. S1). A value of $\beta = 1$ represents direct proportionality between a variable's CO_2 response and the change in CO_2. Where possible (i.e. when reported at source) we report uncertainties as 95% confidence intervals.

As described earlier, attributing iCO_2 as the cause of trends is confounded by covarying factors which also drive variability in the terrestrial carbon sink. We discuss these other global-change factors in the context of attribution, but do not cover them in depth. The difference between direct evidence from eCO_2 experiments and indirect evidence from historical data (concurrent with a suite of global-change factors) motivates our use of two abbreviations: eCO_2 and iCO_2. As with eCO_2 and iCO_2, we distinguish direct CO_2 responses (β_{dir}) from indirect apparent CO_2 'responses' (β_{app}).

II. Theory – a hierarchy of mechanism

1. Direct plant physiological responses to CO_2

Photosynthesis is limited by CO_2 or light (Farquhar *et al.*, 1980). When CO_2 is limiting, theory predicts that eCO_2 increases leaf-scale net carbon assimilation (A_{net}) ($\beta_{dir,hist} = 0.86$, *c.* 280–400 ppm; Table S1). The enzyme that fixes CO_2 (RuBisCO) also catalyses an oxygenation reaction, which results in CO_2 loss (photorespiration; Farquhar *et al.*, 1980). eCO_2 also suppresses photorespiration (Fig. 2a). Given that photorespiration always occurs during C_3 photosynthesis, the suppression of photorespiration by eCO_2 increases A_{net} also when light is limiting, but with a lower response ($\beta_{dir,hist} = 0.31$). Canopy-scale A_{net} results from a mixture of CO_2 and light-limited photosynthesis, and thus has an intermediate eCO_2 response that depends on the fraction of light-saturated leaves in the canopy ($\beta_{dir,hist} = 0.60 \pm 0.3$; Fig. 2c). As $[CO_2]$ increases, the fraction of light-saturated leaves in the canopy is expected to decrease, and therefore the historical eCO_2 response of GPP is expected to be higher than the future response ($\beta_{dir,fut} = 0.46 \pm 0.2$, *c.* 400–550 ppm; Fig 2c).

C_4 plants have evolved to concentrate carbon, thus saturating photosynthesis and suppressing photorespiration at low $[CO_2]$ (Ehleringer & Björkman, 1977). Therefore A_{net} in C_4 plants is not directly influenced by $[CO_2]$ above *c.* 200 ppm (Fig. 2a), although water savings from reduced stomatal conductance (g_s) may stimulate A_{net} indirectly (Leakey *et al.*, 2004).

Photosynthesis requires the acquisition of other resources and eCO_2 stimulation of A_{net} increases A_{net} per unit resource consumption, that is, increases resource use-efficiencies of water (WUE), light (LUE), and leaf nitrogen (Cowan, 1982; Drake *et al.*, 1997). Increased use efficiencies imply a shift in a plant's resource-use economy (Bloom *et al.*, 1985) which is commonly studied using optimization theory.

Optimization theory predicts that a change in the ratio of $A_{net} : g_s$ (iWUE) in proportion to the change in $[CO_2]$ ($\beta_{dir} \approx 1$; Fig. 2d) maximizes the benefit of carbon gain while minimizing the cost of water lost for C_3 (Medlyn *et al.*, 2011) and C_4 plants (Lin *et al.*, 2015). Canopy-scaling theory predicts that the increase in iWUE is preserved at the canopy scale (Fig. 2e). Where the response of A_{net} to eCO_2 is less than proportional ($\beta_{dir} < 1$) the increase in iWUE (i.e. A_{net}/g_s) implies a reduction in g_s (canopy-scale iWUE $\beta_{dir,hist} = 1.1 \pm 0.1$, A_{net} $\beta_{dir,hist} = 0.60 \pm 0.3$, thus g_s $\beta_{dir,hist} = -0.53 \pm 0.2$; Fig. 2f,i). Owing to the lower predicted A_{net} in the future, the predicted decrease in g_s is greater ($\beta_{dir,fut} = -0.62 \pm 0.1$).

Optimization theory also predicts reduction in photosynthetic carboxylation capacity (V_{cmax}), reducing nitrogen demand (Bowes, 1991; Drake *et al.*, 1997). A reduction in leaf nitrogen may also occur as a result of limited plant-available soil nitrogen (Section II.2) or physiological competition for the products of electron transport (Bloom *et al.*, 2012).

2. Plant biomass production

Biomass production of leaf, wood, and root tissues is controlled by the interplay of source (resource acquisition), sink (metabolic tissue production) (Muller *et al.*, 2011; Fatichi *et al.*, 2019), and regulatory processes (phenology, hormones) (Schwartz, 2013; Bahuguna & Jagadish, 2015). Within this framework, eCO_2 can increase BP when BP is either carbon source-limited or when eCO_2 can alleviate other limitations. Plant BP is carbon source-limited when in competition with respiration for available carbon and when light limits BP (Lloyd & Farquhar, 2008). Sustained periods of high growth may also reduce carbon stores (Würth *et al.*, 2005), potentially leading to carbon-source limitation.

Biomass production is also carbon sink-limited by stoichiometric nutrient requirements (Elser *et al.*, 2010). Thus increased BP requires either increased nutrient acquisition or increased stoichiometric carbon-to-nutrient ratios. Increased plant-available carbon may be able to 'pay' for increased nutrient acquisition via a number of mechanisms (e.g. increased fine-root BP, mycorrhizal investment, exudation, atmospheric N fixation) (Luxmoore, 1981; Hungate *et al.*, 1999; Fleischer *et al.*, 2019). Changing stoichiometry may result in feedbacks that compound nutrient limitations by reducing decomposition rates and nutrient availability (Comins & McMurtrie, 1993), known as progressive nitrogen limitation (Luo *et al.*, 2004).

In environments where BP is primarily sink-limited (e.g. tree-lines (temperature limitation), arid and semiarid (water limitation)), increased carbon availability may have little effect on BP (Kramer, 1981; Körner, 2003b). However, in water-limited environments, increased iWUE could increase BP (Mooney *et al.*, 1991; Wullschleger *et al.*, 2002). LAI may also be limited by water availability (Woodward, 1987; Yang *et al.*, 2018) and increased WUE may increase LAI and light absorption, leading to indirect positive feedback on GPP and transpiration (Fatichi *et al.*, 2016; Trancoso *et al.*, 2017).

If BP is restricted by sink limitation, BP efficiency (BP per unit GPP) would decrease and the labile products of photosynthesis would accumulate. If BP is stimulated this may be as short-lived, primary tissues (leaves and fine-roots) or long-lived, secondary tissues (wood) (De Kauwe *et al.*, 2014). Division of carbon among these tissues determines the residence time of carbon in plant biomass. Wood has greater residence time and thus greater potential to increase C_{veg} accumulation over multiple years. Greater production of short-lived tissues (i.e. leaves and fine-roots) may increase resource capture and will increase litter carbon inputs to the soil.

3. Plant mortality

Increases in mortality rates reduce vegetation residence times and have the potential to offset any biomass gains resulting from

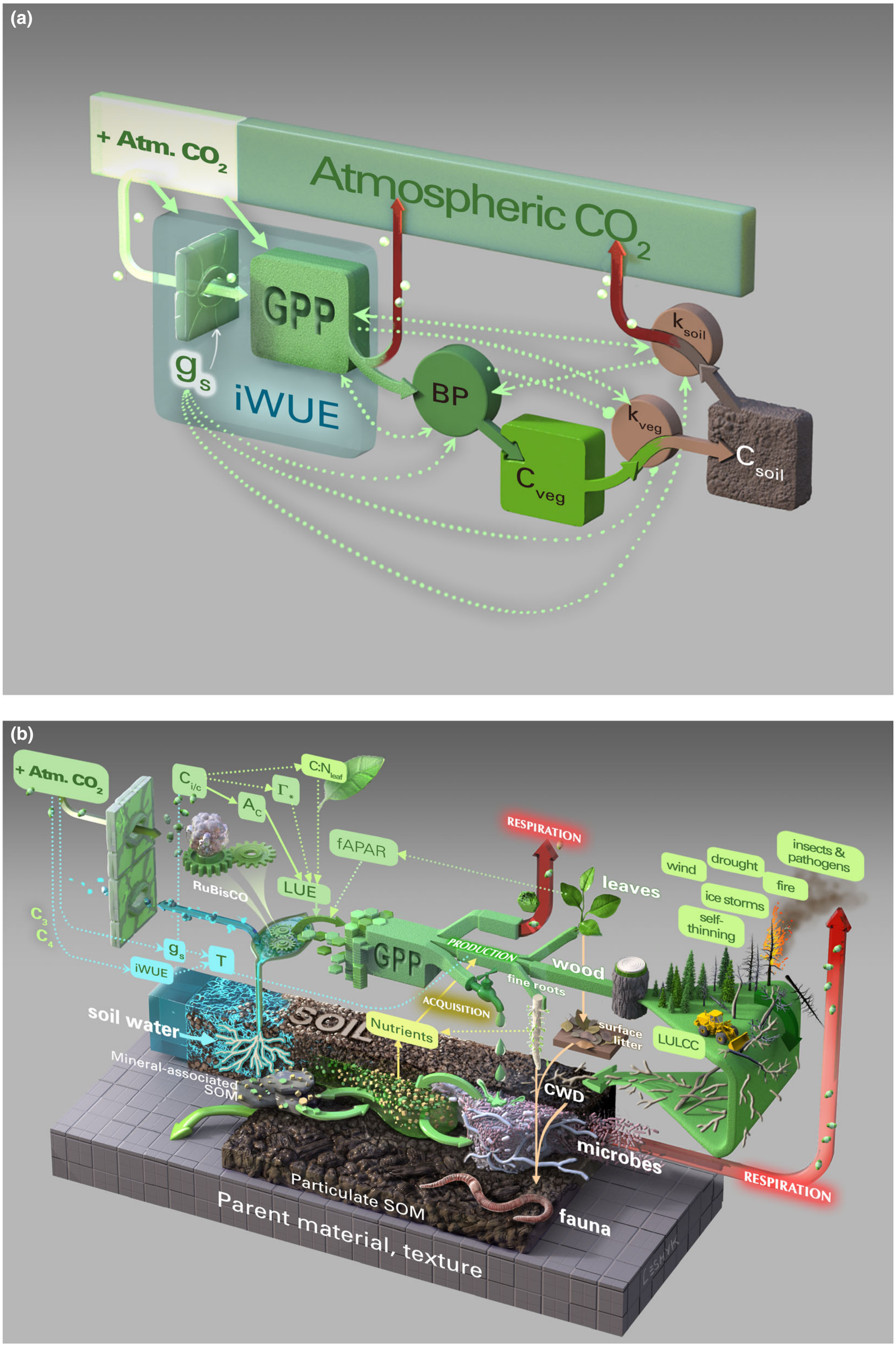

Fig. 1 Conceptual diagrams of the terrestrial carbon cycle and the action of elevated atmospheric [CO_2] (eCO_2). (a) Simple pool and flux (three-dimensional (3D) shapes) diagram of the terrestrial carbon cycle showing key pools, fluxes, and processes relevant to the CO_2-fertilization hypothesis as described in Box 1. Two-dimensional (2D) arrows represent direct (solid) or indirect (dashed) positive influences (triangular arrow heads), or the possibility of both positive and negative (circular) influences of eCO_2. (b) Rich conceptual diagram of a landscape-scale carbon cycle and the influence of eCO_2 showing more processes (see Section II) and their interconnected, multiscale nature. Solid arrows (3D and 2D) represent material (mostly carbon) flows, dotted arrows represent influence. Abbreviations not in Table 1: $C_{i/c}$, internal or chloroplastic [CO_2]; A_c, carboxylation limited photosynthesis; Γ^*, photorespiration; C : N_{leaf}, leaf carbon : nitrogen ratio; T, transpiration; LULCC, land-use and land cover change; CWD, coarse woody debris.

Box 2 Evidence themes.

Theme 1: Direct exposure to elevated CO_2

Experiments in which plants are grown in CO_2-enriched air and observations of plants growing close to geological CO_2 sources provide the only direct evidence of plant and soil responses to future [CO_2]. The first eCO_2 experiments were typically at the scales of leaves or small, individual plants. Ecosystem-scale open-top chambers (OTCs) and larger free-air CO_2 enrichment (FACE) experiments have since been implemented over decades in more natural settings. All of these experiments provide evidence for the direct CO_2 effect on photosynthesis and stomatal conductance. These experiments also provide valuable data on biomass production, allocation to organs, and transpiration. The timescale of most experiments (< 10 yr), however, is generally much shorter than many ecosystem processes, and evidence for CO_2 effects on mortality, plant community dynamics, or changes in soil carbon stocks is limited.

Theme 2: Tree growth measurements

Tree rings and forest inventories provide long-term estimates of wood BP in forest ecosystems across the globe (e.g. Hember *et al*., 2019; Hubau *et al*., 2020). Tree ring data are annually resolved estimates of individual stem growth over the past decades to millennia (e.g. Babst *et al*., 2014). These data provide insights into individual growth variability in relation to environmental changes including soil moisture, temperature and potentially also iCO_2. Repeated inventories of forest ecosystems offer an assessment of forest-scale dynamics and the demographic processes of recruitment, growth, and mortality over previous decades and in some cases around century length (Pretzsch *et al*., 2014). Inventories tend to have a coarser temporal resolution (5–10 yr resurveys) but represent forest-stand spatial scales, albeit that plot scale varies widely: 0.067 ha forest inventory analysis, *c*. 1–2 ha (e.g. Brienen *et al*., 2015; Hubau *et al*., 2020), 50 ha ForestGEO network (e.g. Chave *et al*., 2008).

Theme 3: Ecosystem monitoring

Ecosystem eddy-covariance and global remote sensing may detect effects of iCO_2 on carbon, water, and energy fluxes over recent decades. Tower-based sensors are used to calculate ecosystem-scale (*c*. 1 km) carbon, water, and energy fluxes from the covariance of gas concentrations and vertical wind velocity (Baldocchi, 2003). A global network of continental networks (http://fluxnet.fluxdata.org) synthesizes flux-tower data from 916 sites, some in operation for over two decades, while the majority have run for a decade or less and are located in temperate ecosystems (Chu *et al*., 2017). Satellite and other aircraft-borne Earth observing systems have been measuring the reflectance of electromagnetic radiation from the Earth's surface, used to infer changes in vegetation cover, leaf area, and biomass at a global scale (Fensholt *et al*., 2004; Smith *et al*., 2020). Reflected wavelengths from Landsat (first launched in 1972), MODIS, and other instruments can be used to measure the fraction of absorbed photosynthetically active radiation (fAPAR) and greenness indices, which are further used to infer leaf area index (LAI), GPP, and NPP with the help of simple models (Myneni *et al*., 1997; Field *et al*., 1998). Microwave wavelengths are used to measure vegetation optical depth (VOD, first available in the early 1980s) which can be used to infer vegetation water content and, by extension, vegetation biomass (Liu *et al*., 2015).

Theme 4: Large-scale constraints

At regional-to-global scales, several long-term data streams provide constraints on the global carbon budget and its change over time. These data streams include near-surface and vertical profiles of atmospheric CO_2 concentration and $\delta^{13}C$, global water-cycle measurements, and atmospheric composition from ice cores. Atmospheric CO_2 measurements can be combined with other data and models to infer the global carbon budget and spatial details of land carbon uptake (Peylin *et al*., 2013; Friedlingstein *et al*., 2019). The impact of vegetation responses to iCO_2 on the hydrological cycle measured by stream gauges can also act as further indirect evidence (Ukkola *et al*., 2016; Trancoso *et al*., 2017). Carbonyl sulphide (OCS) can be used to infer global carbon assimilation because it is taken up by plants through stomata and is transformed by carbonic anhydrase (Wohlfahrt *et al*., 2012; Whelan *et al*., 2018).

increased BP (Eqn B3) (Bugmann & Bigler, 2011; Körner, 2017). Hydraulic failure and, to a lesser extent, carbon starvation are thought to be interrelated mechanisms of plant death (McDowell *et al*., 2008). By easing the carbon and hydraulic impacts of abiotic and biotic stressors such as drought, or pest and pathogen attack, eCO_2 could potentially decrease mortality. Greater carbon resources could supply greater maintenance respiration, stored carbon reserves or synthesis of defence compounds (McDowell *et al*., 2008). More efficient water use (Section II.1) could delay the onset or intensity of drought, which could reduce the risk of xylem-conductivity losses.

Indirect influences on mortality may emerge from the acceleration of individual size growth. Increased growth could reduce small-size-related mortality by speeding individuals out of the hazards of early life (e.g. browsing) and increasing their ability to acquire resources (Metcalfe *et al*., 2014; Hülsmann *et al*., 2018). Conversely, increased growth could increase large-size mortality risk, with tall trees being more susceptible to hydraulic stress, windthrow, lightning, and certain pests or pathogens (Bugmann & Bigler, 2011; Bennett *et al*., 2015; Körner, 2017; Trugman *et al*., 2018).

At the stand scale, increased growth may accelerate post-disturbance successional dynamics (McDowell *et al*., 2020). Intensified competition for light, water, and nutrients could lead to earlier reorganization and transition (self-thinning) phases of development (Bormann & Likens, 1979), but also an earlier switch from transition to steady-state phases (Miller *et al*., 2016). Acceleration of stand development by eCO_2 may or may not change self-thinning relationships (tree size to stem density) of a forest stand, with no change leading to no change in biomass. However, acceleration of

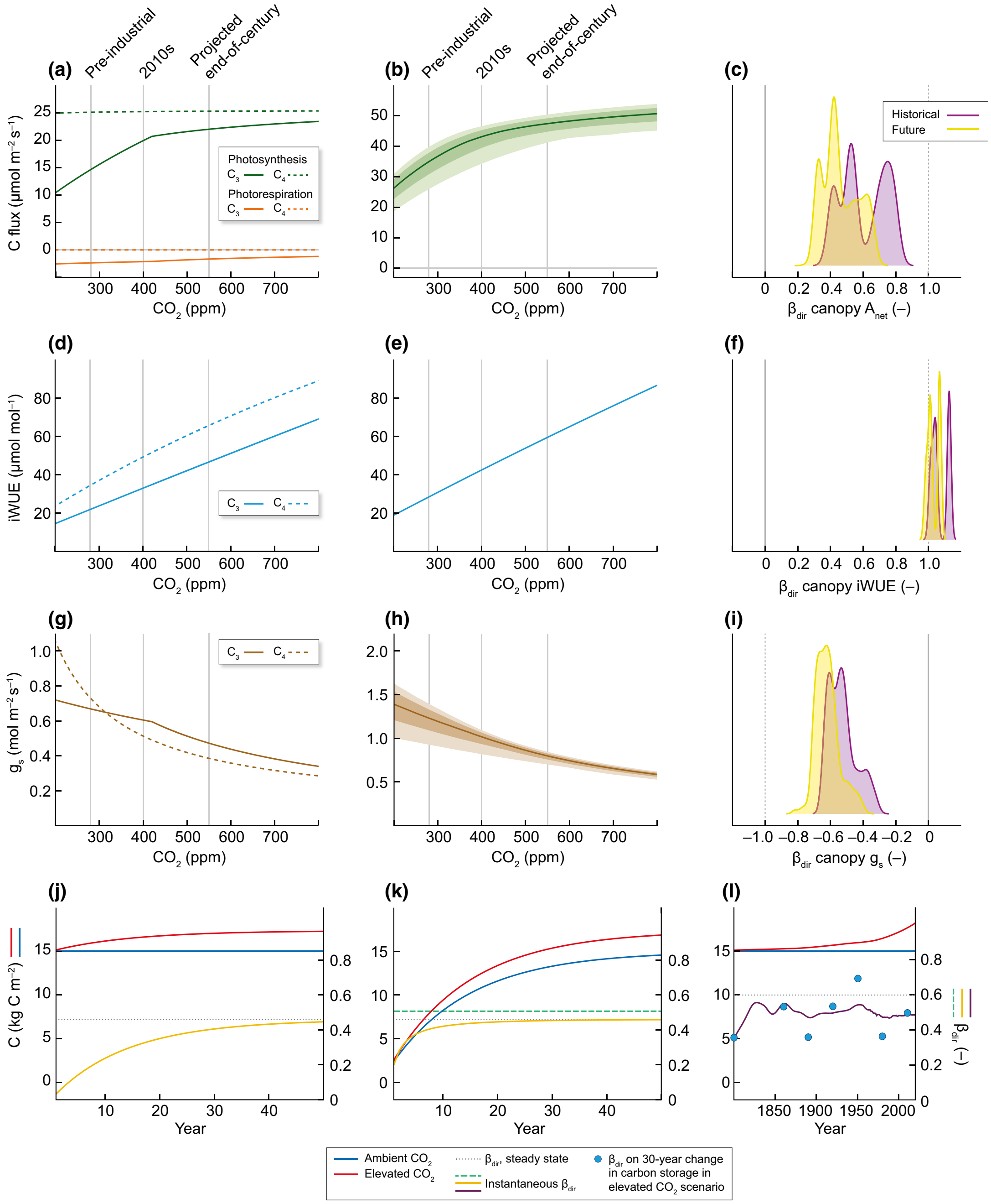

Fig. 2 (a–l) Modelled theoretical responses to atmospheric CO_2 concentration ([CO_2], ppm) of photosynthesis, A_{net} (μmol m^{-2} s^{-1}, dark green) (a–c) and photorespiration (μmol m^{-2} s^{-1}, orange) (a); intrinsic water-use efficiency (iWUE, μmol mol^{-1}) (d–f); stomatal conductance, g_s (mol m^{-2} s^{-1}) (g–i); and carbon storage (kg C m^{-2}) (j–l) under ambient (blue) and elevated (red) [CO_2]. Leaf (a, d, g) and canopy (b, e, h) scale for C_3 (solid line) and C_4 (dashed, leaf-scale only) plants. Variation in (b), (e) and (h) from a 1000-member ensemble (mean, SD, and 95 percentile shown) – a factorial combination of 100 top-of-canopy photosynthetic carboxylation capacity (V_{cmax}) values (mean = 60, SD = 10) and 10 values of the maximum electron transport rate (J_{max}) to V_{cmax} slope (mean = 1.63, SD = 0.2), the iWUE response does not vary in this ensemble. Distributions of direct CO_2 responses (β_{dir}) for historical (purple, 280–400 ppm) and future (yellow, 400–550 ppm) [CO_2] changes (c, f, i) of diurnally integrated, canopy-scale variables that include the same leaf physiology variation as in (b), (e), (h), plus three temperatures (10, 15, 25°C) and relative humidity (50%, 70%, 90%) combined in factorial. Trimodality in the gross primary production (GPP) β distributions results from the temperature variation. β distributions are weighted by the variables' absolute response to CO_2. Carbon storage (j–l) was calculated using a simple one-pool model with the mean future GPP response ($\beta_{dir,fut}$) applied to biomass production (BP) for [CO_2] at 400 and 550 ppm when initial carbon stores are in equilibrium (j) or at 10% of equilibrium (k). (l) Historical response ($\beta_{dir,hist}$) when initial carbon stores are assumed in equilibrium at 280 ppm and using the observed historical CO_2 record. Instantaneous β_{dir} values for absolute carbon storage are shown (j–l, right *y*-axis, yellow or purple), as well as β_{dir} calculated using carbon storage increment (green dashed), and β_{dir} on 30 yr change in carbon storage in elevated CO_2 scenario (blue points). Further modelling details are in Supporting Information Notes S3. Grey vertical lines (a, b, d, e, g, h) relate to pre-industrial era, 2010s, and projected end-of-century [CO_2] (280, 400, 550 ppm). Grey vertical lines (c, f, i) relate β_{dir} of 0 (solid) and 1 or −1 (dotted). Horizontal grey dotted lines (j–l) are β_{dir} when both ambient and elevated CO_2 carbon pools are in a steady state.

stand development could increase biomass at the landscape scale by closing forest gaps more quickly. Differential mortality effects on different plant species could alter competitive dynamics, community composition, and associated stand properties (e.g. among fast-growing, ruderal/pioneer species and more conservative, slow-growing species; Ruiz-Benito *et al.*, 2017).

4. Organic matter decomposition

Residence times of litter and SOM vary from minutes to millenia and can respond rapidly to environmental perturbation (Trumbore, 2009; Schmidt *et al.*, 2011; Dwivedi *et al.*, 2019). Increases in SOM decomposition rates reduce SOM residence times and have the potential to offset any eCO_2-related increases in litter inputs. Accelerated decomposition of litter and particulate SOM (i.e. priming) can result from microbial responses to increased labile-carbon availability (Kuzyakov *et al.*, 2000; Blagodatskaya *et al.*, 2014), including at depth (Fontaine *et al.*, 2007). Organic acids produced by roots can destabilize mineral-associated SOM (Keiluweit *et al.*, 2015). eCO_2 effects on environmental conditions could also affect SOM decomposition. CO_2-related increases in soil water (Section II.1) would probably stimulate decomposition in water-limited ecosystems (Castanha *et al.*, 2018), but could reduce oxygen availability (slowing decomposition) in energy-limited ecosystems.

Microbial activity has also been linked to the formation of mineral-associated SOM (Cotrufo *et al.*, 2013; Liang *et al.*, 2017), and potentially soil aggregates (Ge *et al.*, 2018), which might slow decomposition by restricting microbial access to SOM (Kögel-Knabner *et al.*, 2008). Changing litter stoichiometry might slow decomposition (Section II.2). Roots can distribute carbon deeper in the soil where decomposition is slower and capacity for mineral stabilization is higher (Jackson *et al.*, 2017; Hicks Pries *et al.*, 2018).

Greater decomposition rates might also increase soil nutrient availability, potentially reducing plant nutrient limitation (Treseder, 2004; Dijkstra, 2008) or increasing microbial immobilization. Over longer timescales, nutrient immobilization can reduce nutrient losses, leading to accumulation of ecosystem nutrient stocks which may enhance mineralization and progressively release plants from nutrient limitation (Rastetter *et al.*, 1997; Walker *et al.*, 2015).

5. Terrestrial ecosystem carbon responses to CO_2

The response of terrestrial carbon storage to eCO_2 (ΔC_{eco}) is the net result of the above described processes. Potential increases in BP and litter production are balanced by potential increases in loss rates (Eqns B3 and B4). Increased BP of short-lived primary tissues such as leaves and fine roots could lead to greater biomass of these transient C_{veg} pools and to increased litter inputs to the soil. If wood BP is stimulated by eCO_2, over medium timescales (annual to several decades) ecosystem biomass could increase as a result of the longer residence time of wood. However, wood BP is tied to tree size growth rates and the effects of tree size on mortality rates may be either positive or negative (Section II.3). Greater wood BP or greater wood mortality rates would result in greater coarse woody debris, which may immobilize nutrients (e.g. Zimmerman *et al.*, 1995).

Increased plant inputs to litter and soil (e.g. wood, leaf and root litter, root exudates, and mycorrhizal subsidies) could increase C_{soil}. However, the complex processes that drive the formation and decomposition of SOM make the response of C_{soil} to eCO_2 difficult to predict (Schmidt *et al.*, 2011; Dwivedi *et al.*, 2019; Section II.4). Increased soil mineralization rates could lead to greater C_{eco} if nutrients are redistributed from soils to plants, which have higher carbon: nutrient ratios and hence can store more carbon per unit nutrient (Rastetter *et al.*, 1992; Zaehle *et al.*, 2014).

A one-pool ecosystem carbon model (Box 1) with simplifying assumptions (BP β_{dir} = GPP β_{dir}; residence time $\beta_{dir} = 0$) provides baseline-expected β_{dir} for carbon storage (Fig. 2j–l). The model indicates that when starting carbon storage is nonzero, β_{dir} depends on the time of measurement (Fig. 2j,k). Based on the observed [CO_2] trend (Le Quéré *et al.*, 2018), the model indicates that β_{dir} calculations over a 30 yr period (typical of forest-inventory analysis) are generally a little smaller ($\beta_{dir,hist} \approx 0.5$) than steady-state ($\beta_{dir,hist} = 0.6$; Fig 2l). Departures from these expected β values derived from GPP responses alone provide a guide to the magnitude of positive and negative feedbacks in eCO_2 studies and can help to guide iCO_2 attribution in historical studies.

III. The evidence

1. Physiology

Carbon assimilation and GPP Evidence across FACE experiments (11 sites, 45 species) shows that eCO_2 increased leaf-level, light-saturated photosynthesis ($\beta_{dir} = 0.73 \pm 0.2$; see Notes S3 for methods), and supports differences between C_3 ($\beta_{dir} = 0.79 \pm 0.2$) and C_4 species ($\beta_{dir} = 0.27 \pm 0.2$) (Ainsworth & Long, 2005; all reported β values are in Table 2). Evidence suggests that maximum photosynthetic capacity acclimated (reduced) to eCO_2, primarily maximum carboxylation capacity ($\beta_{dir} = -0.38 \pm 0.1$) (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007). Nevertheless, in many forest eCO_2 experiments, photosynthetic stimulation (> 5 yr) was only minimally affected by acclimation (Crous *et al.*, 2008; Bader *et al.*, 2010; Ellsworth *et al.*, 2017).

Indirect evidence also suggests increased photosynthesis with iCO_2. Deuterium isotopomers of glucose in plant archives indicate that the leaf-level photorespiration: assimilation ratio has decreased since pre-industrial times ($\beta_{app} = -0.99$) (Ehlers *et al.*, 2015), which translates to an increase in photosynthesis ($\beta_{app} = 1.0$) (Ehlers *et al.*, 2015). GPP estimates from eddy-covariance (23 sites, *c.* 20 yr) suggest a recent increase ($\beta_{app} = 1.6 \pm 0.9$), attributing a substantial iCO_2 contribution ($\beta_{dir,hist} = 1.2 \pm 0.6$) (Fernández-Martínez *et al.*, 2017). Eddy-covariance data used to calibrate a model suggests a lower iCO_2 response ($\beta_{dir,hist} = 0.5 \pm 0.2$) (Ueyama *et al.*, 2020).

Ice-core measurements of atmospheric carbonyl sulfide (OCS) combined with mass-balance analysis suggests that global GPP has increased since pre-industrial times ($\beta_{app} = 0.95 \pm 0.2$) (Campbell *et al.*, 2017), as do ice-core measurements of atmospheric O_2

Table 2 CO_2 responses across studies.

Process	eCO_2/iCO_2	Study	Variable	Study type, location	Species, genus, biome	Plotted as	Start year†	End year†	Ambient/ start CO_2	Elevated/ end CO_2	Variable response ratio	95% CI	CO_2 response ratio	95% CI	β	95% CI
GPP	iCO_2	Ehlers *et al*. (2015)	A:gstar	Herbarium 2H isotopomers	*Brassica, Sphagnum, Eriophorum*	–	1890	2012	293.46	391.88	–25	–	34	–	–0.99	–
GPP	iCO_2	Ehlers *et al*. (2015)	Asat	Herbarium 2H isotopomers model	*Brassica, Sphagnum, Eriophorum*	GPP	1890	2012	293.46	391.88	35	–	34	–	1	–
GPP	eCO_2	Ainsworth & Long (2005)	Asat	FACE meta-analysis	Temperate	GPP	–	–	380	550	28	4.9	45	5.6	0.68	0.13
GPP	eCO_2	Ainsworth & Long (2005)	Asat	FACE meta-analysis	Temperate	–	–	–	380	550	29	4.4	45	5.6	0.7	0.12
GPP	eCO_2	Ainsworth & Long (2005)	Asat	FACE meta-analysis	Temperate	–	–	–	380	550	7	22	45	5.6	0.18	0.57
GPP	iCO_2	Campbell *et al*. (2017)	GPP	Ice-core OCS	Global	GPP	1900	2013	296.57	394.6	31	5	33	2.8	0.95	0.15
GPP	iCO_2	Cheng *et al*. (2017)	GPP	RS ET WUE model	Global best estimate	GPP	1982	2011	340.47	389.79	15	6.2	14	2.2	1.1	0.43
GPP	iCO_2	Ciais *et al*. (2012)	GPP	Ice-core 18O	Global	GPP	1760	2010	276.58	387.99	54	120	40	3.1	1.3	2.3
GPP	iCO_2	Fernandez-Martinez *et al*. (2017)	GPP	Flux-tower	Temperate	GPP	1992	2013	355.4	394.6	18	8.2	11	2.1	1.6	0.72
GPP	iCO_2_CO_2att.	Fernandez-Martinez *et al*. (2017)	GPP	Flux-tower, CO_2 attribution	Temperate	GPP	1992	2013	355.4	394.6	13	4.5	11	2.1	1.2	0.44
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Flux-tower upscaled method 1	Global	GPP	2000	2014	368.23	396.7	–2.8	2.1	7.7	2	–0.39	0.3
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Flux-tower upscaled method 2	Global	GPP	2000	2014	368.23	396.7	–1.9	1.9	7.7	2	–0.25	0.27
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Flux-tower upscaled method 3	Global	GPP	2000	2014	368.23	396.7	–2.2	1.6	7.7	2	–0.29	0.24
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	RS fAPAR LUE model method 1	Global	GPP	2000	2014	368.23	396.7	6.2	6.3	7.7	2	0.8	0.82
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	RS fAPAR LUE model method 2	Global	GPP	2000	2014	368.23	396.7	9.6	3.4	7.7	2	1.2	0.52
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	RS fAPAR LUE model method 3	Multi-biome	GPP	2000	2014	368.23	396.7	4	4.3	7.7	2	0.53	0.57
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	RS fAPAR LUE model method 4	Multi-biome	GPP	2000	2014	368.23	396.7	0.11	3.3	7.7	2	0.014	0.44
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	RS fAPAR LUE model method 5	Global	GPP	2000	2014	368.23	396.7	5.6	3.5	7.7	2	0.73	0.48
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Process model 1	Global	GPP	2000	2014	368.23	396.7	12	5.8	7.7	2	1.6	0.79
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Process model 2	Global	GPP	2000	2014	368.23	396.7	4.4	5.4	7.7	2	0.57	0.72
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Vegetation index method 1	Global	GPP	2000	2014	368.23	396.7	7.5	4.4	7.7	2	0.98	0.6
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Vegetation index method 2	Global	GPP	2000	2014	368.23	396.7	2.3	2.7	7.7	2	0.31	0.36
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Vegetation index method 3	Global	GPP	2000	2014	368.23	396.7	6	3.6	7.7	2	0.78	0.5
GPP	iCO_2_CO_2att.	Sun *et al*. (2019)	GPP	Vegetation index method 4	Global	GPP	2000	2014	368.23	396.7	5.5	4.8	7.7	2	0.72	0.63
GPP	iCO_2_CO_2att.	Ueyama *et al*. (2020)	GPP	Flux-tower constrained model, CO_2 attribution	Multi-biome	GPP	1990	2014	353.2	396.7	6	0.3	12	2.1	0.5	0.086

Table 2 (Continued)

Process	eCO_2/iCO_2	Study	Variable	Study type, location	Species, genus, biome	Plotted as	Start year[†]	End year[†]	Ambient/ start CO_2	Elevated/ end CO_2	Variable response ratio	95% CI	CO_2 response ratio	95% CI	β	95% CI
GPP	eCO_2	Ainsworth & Long (2005)	gs	FACE meta-analysis	Temperate	–	–	–	380	550	–20	2.7	45	5.6	–0.6	0.11
GPP	eCO_2	Gimeno *et al*. (2015)	gs	FACE EucFACE	*Eucalyptus tereticornis*	–	–	–	400	550	–28	25	38	5.3	–1	1.1
GPP	eCO_2	Medlyn *et al*. (2001	gs	eCO_2 meta-analysis	All	–	–	–	350	700	–14	9	100	6.4	–0.22	0.15
GPP	iCO_2_CO_2att.	Ueyama *et al*. (2020)	gs	Flux-tower constrained model, CO_2 attribution	Multi-biome	–	1990	2014	353.2	396.7	–3.2	0.26	12	2.1	–0.28	0.051
GPP	eCO_2	Ainsworth & Long (2005)	iWUE	FACE meta-analysis	Temperate	WUE	–	–	380	550	54	17	45	5.6	1.2	0.33
GPP	eCO_2	Barton *et al*. (2012)	iWUE	Whole tree chamber	*Eucalyptus saligna*	WUE	–	–	384.15	624.15	61	12	62	5.6	0.98	0.17
GPP	eCO_2	Battipaglia *et al*. (2013)	iWUE	FACE Duke	*Liquidambar styraciflua*	WUE	–	–	381	546	75	26	43	5.6	1.6	0.45
GPP	eCO_2	Battipaglia *et al*. (2013)	iWUE	FACE Duke	*Pinus taeda*	–	–	–	375	556	77	–	48	–	1.4	–
GPP	eCO_2	Battipaglia *et al*. (2013)	iWUE	FACE ORNL	*Liquidambar styraciflua*	–	–	–	383	533	56	–	39	–	1.3	–
GPP	iCO_2_CO_2att.	Frank *et al*. (2015)	iWUE	Tree-ring	*Pinus*	WUE	1905	1997	297.87	362.51	22	12	22	2.6	1	0.51
GPP	iCO_2_CO_2att.	Frank *et al*. (2015)	iWUE	Tree-ring	*Quercus*	WUE	1905	1997	297.87	362.51	14	20	22	2.6	0.67	0.9
GPP	iCO_2	Keeling *et al*. (2017)	iWUE	Atmospheric 13C	Global	WUE	1900	1999	296.57	367.06	20	18	24	2.7	0.85	0.71
GPP	iCO_2	Penuelas *et al*. (2011)	iWUE	Tree-ring	Forests	WUE	1965	2005	319.56	378.23	20	13	18	2.4	1.1	0.64
GPP	iCO_2	Saurer *et al*. (2004)	iWUE	Tree-ring	*Larix*	WUE	1875	1975	288.97	330.28	17	38	14	2.6	1.2	2.5
GPP	iCO_2	Saurer *et al*. (2004)	iWUE	Tree-ring	*Picea*	WUE	1875	1975	288.97	330.28	23	25	14	2.6	1.5	1.6
GPP	iCO_2	Saurer *et al*. (2004)	iWUE	Tree-ring	*Pinus*	WUE	1875	1975	288.97	330.28	17	31	14	2.6	1.2	2
GPP	iCO_2_CO_2att.	Ueyama *et al*. (2020)	iWUE	Flux-tower constrained model, CO_2 attribution	Multi-biome	WUE	1990	2014	353.2	396.7	8.8	0.26	12	2.1	0.73	0.12
GPP	iCO_2	van der Sleen *et al*. (2015)	iWUE	Tree-ring	Multi-site-tropical	WUE	1864	2014	286.71	396.7	32	–	38	–	0.87	–
GPP	eCO_2	Ainsworth & Long (2005)	N_leaf_area	FACE meta-analysis	Temperate	–	–	–	380	550	–4.9	2.6	45	5.6	–0.14	0.075
GPP	eCO_2	Ainsworth & Long (2005)	v_cmax	FACE meta-analysis	Temperate	–	–	–	380	550	–13	2.5	45	5.6	–0.38	0.087
GPP	eCO_2	DeKauwe *et al*. (2013)	T	FACE Duke	Pinus taeda	–	–	–	375	556	1	–	48	–	0.027	–
GPP	eCO_2	DeKauwe *et al*. (2013)	T	FACE ORNL	*Liquidambar styraciflua*	–	–	–	383	533	–16	–	39	–	–0.54	–
GPP	eCO_2	DeKauwe *et al*. (2013)	WUE	FACE Duke	*Pinus taeda*	WUE	–	–	375	556	29	18	48	5.7	0.65	0.36
GPP	eCO_2	DeKauwe *et al*. (2013)	WUE	FACE ORNL	*Liquidambar styraciflua*	WUE	–	–	383	533	32	26	39	5.5	0.84	0.6
GPP	iCO_2	FACE EucFACETang *et al*. (2014)	WUE	RS GPP and ET model	Global	–	2000	2013	368.23	394.6	–3.4	–	7.2	–	–0.49	–
GPP	iCO_2	Xue *et al*. (2015)	WUE	RS GPP and ET model	Global	–	2000	2013	368.23	394.6	1.9	–	7.2	–	0.28	–
GPP	iCO_2	Keenan *et al*. (2013)	WUE_inherent	Flux-towers	Multi-site-temperate	WUE	1992	2010	355.4	387.99	41	23	9.2	2.1	3.9	2.1
GPP	iCO_2	Mastrotheodorus *et al*. (2017)	WUE_inherent	Flux-towers	Multi-site-temperate	WUE	1999	2014	367.06	396.7	20	15	8.1	2	2.4	1.7
GPP	iCO_2_CO_2att.	Ueyama *et al*. (2020)	gs	Flux-tower constrained model, CO_2 attribution	Multi-biome	–	1990	2014	353.2	396.7	–3.2	0.26	12	2.1	–0.28	0.051

Table 2 (Continued)

Process	eCO_2/iCO_2	Study	Variable	Study type, location	Species, genus, biome	Plotted as	Start year[†]	End year[†]	Ambient/ start CO_2	Elevated/ end CO_2	Variable response ratio	95% CI	CO_2 response ratio	95% CI	β	95% CI
GPP	iCO_2_CO_2att.	Ueyama *et al.* (2020)	iWUE	Flux-tower constrained model, CO_2 attribution	Multi-biome	WUE	1990	2014	353.2	396.7	8.8	0.26	12	2.1	0.73	0.12
BP	eCO_2	Körner *et al.* (2005)	BAI	FACE Swiss canopy crane	*Fagus*	BP	2001	2003	380	550	13	94	45	5.6	0.32	2.2
BP	eCO_2	Körner *et al.* (2005)	BAI	FACE Swiss canopy crane	*Fagus*	–	2001	–	380	550	93	160	45	5.6	1.8	2.2
BP	eCO_2	Körner *et al.* (2005)	BAI	FACE Swiss canopy crane	*Fagus*	–	2002	–	380	550	39	150	45	5.6	0.89	2.9
BP	eCO_2	Körner *et al.* (2005)	BAI	FACE Swiss canopy crane	*Fagus*	–	2003	–	380	550	91	180	45	5.6	1.8	2.5
BP	eCO_2	Klein *et al.* (2016)	BAI	FACE Swiss spruce	*Picea abies*	BP	–	–	420	554	–8	17	32	5	–0.3	0.67
BP	eCO_2	Norby (1999)	BAI	eCO_2 spring Rapolano	*Quercus ilex*	BP	–	–	345	650	19	–	88	–	0.27	–
BP	eCO_2	Hovenden *et al.* (2019)	BP	FACE synthesis	grassland	BP	–	–	375	618	9	3.4	65	5.8	0.17	0.064
BP	eCO_2	Norby *et al.* (2005)	BP	FACE synthesis	Temperate forest	BP	–	–	377	546	23	4	45	5.6	0.56	0.11
BP	eCO_2	Walker *et al.* (2019)	BP	FACE meta-analysis	Temperate forest	BP	–	–	377	576	23	12	53	5.7	0.49	0.24
BP	eCO_2	Ellsworth *et al.* (2017)	BP_abg	FACE EucFACE	*Eucalyptus tereticornis*	BP	–	–	399	549	–8	17	38	5.3	–0.26	0.58
BP	eCO_2	Nie *et al.* (2013)	BP_fine-root	eCO_2 meta-analysis	Multi-biome	–	–	–	360	645	39	–	79	–	0.56	–
BP	eCO_2	Nowak *et al.* (2004)	BP_fine-root	eCO_2 meta-analysis	Forest	–	–	–	380	675	70	–	78	–	0.92	–
BP	eCO_2	Nowak *et al.* (2004)	BP_fine-root	eCO_2 meta-analysis	Grassland	–	–	–	380	675	11	–	78	–	0.18	–
BP	iCO_2	Brienen *et al.* (2015)	BP_wood	Inventory	Amazon	BP	1983	2011	342.01	389.79	17	6.8	14	2.2	1.2	0.48
BP	iCO_2	Hubau *et al.* (2020)	BP_wood	Inventory	Tropical Africa	BP	1983	2014	342.01	396.7	11	10	16	2.2	0.69	0.63
BP	iCO_2_CO_2att.	Hubau *et al.* (2020)	BP_wood	Inventory, CO_2 attribution	Tropical Africa	BP	1983	2014	342.01	396.7	8.3	16	16	2.2	0.54	0.97
BP	iCO_2	Yu *et al.* (2019)	BP_wood_abv	Inventory	Boreal	–	2001	2008	369.79	384.15	3.6	8.3	3.9	1.9	0.92	2.1
BP	iCO_2	Yu *et al.* (2019)	BP_wood_abv	Inventory	Panbiome	BP	1990	2008	353.2	384.15	8.2	9.4	8.8	2.1	0.94	1.1
BP	iCO_2	Yu *et al.* (2019)	BP_wood_abv	Inventory	Temperate	–	1990	2004	353.2	376.12	27	21	6.5	2.1	3.8	2.9
BP	iCO_2	Yu *et al.* (2019)	BP_wood_abv	Inventory	Tropical	–	1994	2009	357.62	385.81	2.1	6.7	7.9	2.1	0.27	0.86
BP	eCO_2	Ainsworth & Long (2005)	SLA	FACE meta-analysis	Temperate	–	–	–	380	550	–5.9	2.2	45	5.6	–0.16	0.066
BP	eCO_2	Hattenschwiler *et al.* (1997)	TRW	eCO_2 spring Laiatico	*Quercus ilex*	–	1	–	320	650	41	–	100	–	0.49	–
BP	eCO_2	Hattenschwiler *et al.* (1997)	TRW	eCO_2 spring Rapolano	*Quercus ilex*	–	1	–	320	650	77	–	100	–	0.81	–
BP	iCO_2	Voelker *et al.* (2006)	TRW	Tree-ring	*Quercus Pinus*, 1st year	–	1851	1967	286.51	321.62	47	–	12	–	3.3	–
BP	iCO_2	Voelker *et al.* (2006)	TRW	Tree-ring	*Quercus Pinus*, 50th year	BP	1879	2002	289.77	371.93	32	–	28	–	1.1	–
BP	eCO_2	Bader *et al.* (2013)	TRW	FACE Swiss canopy crane	*Fagus*	BP	–	–	380	550	–3.5	51	45	5.6	–0.097	1.4
BP	eCO_2	Bader *et al.* (2013)	TRW	FACE Swiss canopy crane	*Fagus*	–	–	–	380	550	–13	33	45	5.6	–0.38	1
BP	eCO_2	Bader *et al.* (2013)	TRW	FACE Swiss canopy crane	*Fagus*	–	–	–	380	550	–9	24	45	5.6	–0.26	0.71
BP	eCO_2	Bader *et al.* (2013)	TRW	FACE Swiss canopy crane	*Fagus*	–	–	–	380	550	16	59	45	5.6	0.4	1.4
BP	eCO_2	Bader *et al.* (2013)	TRW	FACE Swiss canopy crane	*Quercus*	BP	–	–	380	550	22	75	45	5.6	0.55	1.7
BP	iCO_2	Penuelas *et al.* (2011)	TRW	Tree-ring synthesis	Forests	BP	1965	2005	319.56	378.23	3.9	14	18	2.4	0.23	0.8

Table 2 (Continued)

Process	eCO_2/iCO_2	Study	Variable	Study type, location	Species, genus, biome	Plotted as	Start year†	End year†	Ambient/ start CO_2	Elevated/ end CO_2	Variable response ratio	95% CI	CO_2 response ratio	95% CI	β	95% CI
k_veg	iCO_2	Peng *et al*. (2011)	k_veg_stem	Inventory	Canada	k_veg	1978	1999	334.57	367.06	99	–	9.7	–	7.4	–
k_veg	iCO_2	Pretzsch *et al*. (1997)	k_veg_stem	Inventory	*Fagus sylvatica*	k_veg	1960	2000	316.57	368.23	–17	–	16	–	–1.2	–
k_veg	iCO_2	van Mantgem *et al*. (2009)	k_veg_stem	Inventory	Western North America	k_veg	1981	2004	339.3	376.12	90	23	11	2.2	6.2	1.7
k_veg	iCO_2	Brienen *et al*. (2015	k_veg_stem	tropical_amazon_stems	Amazon	–						–		–		–
k_veg	eCO_2	van Groenigen *et al*. (2014)	LP_veg_abg	eCO_2 meta-analysis	Multi-species	–	–	–	400	625	20	5.5	56	5.4	0.4	0.11
k_veg	iCO_2	Brienen *et al*. (2015	LP_wood	Inventory	Amazon	k_veg	1983	2011	342.01	389.79	38	24	14	2.2	2.5	1.4
k_veg	iCO_2	Hubau *et al*. (2020)	LP_wood	Inventory	Tropical Africa	k_veg	1983	2014	342.01	396.7	–12	29	16	2.2	–0.88	2.2
k_veg	iCO_2_CO_2att.	Hubau *et al*. (2020)	LP_wood	Inventory	Tropical Africa	k_veg	1983	2014	342.01	396.7	30	68	16	2.2	1.8	3.6
k_veg	iCO_2	Yu *et al*. (2019)	LP_wood_abv	Inventory	Boreal	–	2001	2008	369.79	384.15	6.3	–	3.9	–	1.6	–
k_veg	iCO_2	Yu *et al*. (2019)	LP_wood_abv	Inventory	Panbiome	k_veg	1990	2008	353.2	384.15	29	26	8.8	2.1	3	2.5
k_veg	iCO_2	Yu *et al*. (2019)	LP_wood_abv	Inventory	Temperate	–	1990	2004	353.2	376.12	28	–	6.5	–	3.9	–
k_veg	iCO_2	Yu *et al*. (2019)	LP_wood_abv	Inventory	Tropical	–	1994	2009	357.62	385.81	28	–	7.9	–	3.3	–
k_soil	eCO_2	Phillips *et al*. (2011)	C_exudate	FACE Duke, unfertilised	*Pinus taeda*	k_soil	–	–	375	556	56	32	48	5.7	1.1	0.53
k_soil	eCO_2	Bader *et al*. (2010)	C_microbe	FACE Swiss canopy crane	temperate forest	k_soil	–	–	380	550	16	17	45	5.6	0.4	0.39
k_soil	eCO_2	Phillips *et al*. (2011)	C_microbe	FACE Duke, unfertilised	*Pinus taeda*	k_soil	–	–	375	556	56	80	48	5.7	1.1	1.3
k_soil	eCO_2	Cheng *et al*. (2012)	k_soil	FACE	*Avena fatua* AFM	k_soil	–	–	380	580	80	–	53	–	1.4	–
k_soil	eCO_2	van Groenigen *et al*. (2014)	k_soil	eCO_2 meta-analysis	Multi-species	k_soil	–	–	400	625	17	7.3	56	5.4	0.34	0.14
k_soil	eCO_2	Zak *et al*. (2003)	N_immobilisation	FACE synthesis	Temperate forest	–	–	–	380	550	15	71	45	5.6	0.37	1.7
k_soil	eCO_2	Zak *et al*. (2003)	N_mineralisation_gross	FACE synthesis	temperate forest	k_soil	–	–	380	550	13	54	45	5.6	0.33	1.3
k_soil	iCO_2	Fernandez-Martinez *et al*. (2017)	R_eco	Flux-tower synthesis	Multi-biome	k_soil	1992	2013	355.4	394.6	6.3	11	11	2.1	0.58	0.98
k_soil	iCO_2	BondLamberty *et al*. (2018)	R_h_to_R_soil_ratio	synthesis	Global	–	1990	2014	353.2	396.7	17	–	12	–	1.3	–
k_soil	eCO_2	Bader *et al*. (2010)	R_soil	FACE Swiss canopy crane	Temperate forest	k_soil	–	–	380	550	–6.5	25	45	5.6	–0.18	0.71
k_soil	iCO_2	Bond-Lamberty & Thomson (2010)	R_soil	synthesis	Global	k_soil	1989	2008	352.02	384.15	2	–	9.1	–	0.22	–
k_soil	eCO_2	Drake *et al*. (2016)	R_soil	FACE EucFACE	*Eucalyptus tereticornis*	–	–	–	400	430	10	–	7.5	–	1.3	–
k_soil	eCO_2	Drake *et al*. (2016)	R_soil	FACE EucFACE	*Eucalyptus tereticornis*	–	–	–	400	550	10	–	38	–	0.3	–
k_soil	eCO_2	Drake *et al*. (2018)	R_soil	FACE EucFACE	*Eucalyptus tereticornis*	k_soil	–	–	400	550	7	–	38	–	0.21	–
k_soil	eCO_2	Bader *et al*. (2010)	SWC	FACE Swiss canopy crane	Temperate forest	–	–	–	380	550	8.5	–	45	–	0.22	–
NEP	eCO_2	Evans *et al*. (2014)	C_eco	FACE NDFF	Desert	C_eco	–	–	375	513	14	18	37	5.6	0.41	0.52
NEP	iCO_2	Friedlingstein *et al*. (2019)	C_eco	Carbon budget, lower estimate	Global	C_eco	1959	2018	315.66	407.38	7.7	–	29	–	0.29	–
NEP	iCO_2	Friedlingstein *et al*. (2019)	C_eco	Carbon budget, upper estimate	Global	C_eco	1959	2018	315.66	407.38	4.8	–	29	–	0.18	–
NEP	eCO_2	Hungate *et al*. (2013)	C_eco	FACE KSCO	Oak scrub	C_eco	–	–	380	700	3.5	12	84	5.8	0.057	0.19
NEP	iCO_2	Pan *et al*. (2011)	C_eco	Inventory, upscaled	Global forests	C_eco	1990	2007	353.2	382.25	8.3	2.8	8.2	2.1	1	0.41
NEP	iCO_2	Pan *et al*. (2011)	C_eco	Inventory, upscaled	Global, intact forests	C_eco	1990	2007	353.2	382.25	5.4	1.9	8.2	2.1	0.66	0.28
NEP	eCO_2	Iversen *et al*. (2012)	C_fine-root	FACE ORNL, 0-90cm	*Liquidambar styraciflua*	–	–	–	383	533	57	61	39	5.5	1.4	1.2
NEP	iCO_2	Pan *et al*. (2011)	C_litter	Inventory, upscaled	Global	C_soil	1990	1999	353.2	367.06	3.6	–	3.9	–	0.92	–
NEP	eCO_2	Evans *et al*. (2014)	C_soil	FACE NDFF	Desert	C_soil	–	–	375	513	20	23	37	5.6	0.59	0.6

Table 2 (Continued)

Process	eCO_2/iCO_2	Study	Variable	Study type, location	Species, genus, biome	Plotted as	Start year[†]	End year[†]	Ambient/ start CO_2	Elevated/ end CO_2	Variable response ratio	95% CI	CO_2 response ratio	95% CI	β	95% CI
NEP	eCO_2	Hungate *et al*. (2009)	C_soil	eCO_2 meta-analysis	Multi-biome	–	–	–	380	550	1.4	1.1	45	5.6	0.039	0.03
NEP	eCO_2	Hungate *et al*. (2009)	C_soil	eCO_2 meta-analysis, natural studies	Multi-biome	C_soil	–	–	380	550	0.2	1.1	45	5.6	0.0054	0.03
NEP	eCO_2	Hungate *et al*. (2013)	C_soil	FACE KSCO	Oak scrub	C_soil	–	–	380	700	–8.8	27	84	5.8	–0.15	0.49
NEP	eCO_2	Iversen *et al*. (2012)	C_soil	FACE ORNL, 0-90cm	*Liquidambar styraciflua*	C_soil	–	–	383	533	19	23	39	5.5	0.51	0.59
NEP	eCO_2	Jastrow *et al*. (2005)	C_soil	eCO_2 meta-analysis	Meta-analysis	C_soil	–	–	380	550	5.6	2.8	45	5.6	0.15	0.073
NEP	eCO_2	Lajtha *et al*. (2014)	C_soil	Litter addition, Noe	Temperate	–	–	–	350	700	29	13	100	6.4	0.37	0.15
NEP	eCO_2	Lajtha *et al*. (2014)	C_soil	Litter addition, Wingra	Temperate	–	–	–	350	700	33	28	100	6.4	0.41	0.3
NEP	iCO_2	Pan *et al*. (2011)	C_soil	Inventory, 1m, upscaled	Global	C_soil	1990	1999	353.2	367.06	1.2	–	3.9	–	0.31	–
NEP	eCO_2	Zaehle *et al*. (2014)	C_soil	FACE ORNL	*Liquidambar styraciflua*	C_soil	–	–	383	533	2.2	–	39	5.5	0.066	–
NEP	eCO_2	Iversen *et al*. (2012)	c_soil_maom	FACE ORNL, 0-90cm	*Liquidambar styraciflua*	–	–	–	383	533	13	51	39	5.5	0.38	1.4
NEP	eCO_2	Iversen *et al*. (2012)	C_soil_pom	FACE ORNL, 0-90cm	*Liquidambar styraciflua*	–	–	–	383	533	25	41	39	5.5	0.68	0.99
NEP	iCO_2	Chave *et al*. (2008)	C_veg	Inventory	Tropical forest	C_veg	1985	2005	344.99	378.23	2.8	1.9	9.6	2.2	0.3	0.21
NEP	iCO_2	Chave *et al*. (2008)	C_veg	Inventory	Tropical forest, ex. Sinharaja	–	1985	2005	344.99	378.23	3.8	2	9.6	2.2	0.4	0.23
NEP	iCO_2	Friedlingstein *et al*. (2019)	C_veg	Carbon budget, lower estimate	Global	C_veg	1959	2018	315.66	407.38	43	–	29	–	1.4	–
NEP	iCO_2	Friedlingstein *et al*. (2019)	C_veg	Carbon budget, upper estimate	Global	C_veg	1959	2018	315.66	407.38	27	–	29	–	0.93	–
NEP	eCO_2	Hungate *et al*. (2013)	C_veg	FACE KSCO	Oak scrub	C_veg	–	–	380	700	23	14	84	5.8	0.33	0.19
NEP	iCO_2	Pan *et al*. (2011)	C_veg	Inventory, upscaled	Global forests	C_veg	1990	1999	353.2	367.06	7.7	–	3.9	–	1.9	–
NEP	iCO_2	Pretzsch *et al*. (1997)	C_veg	Inventory	*Fagus sylvatica*	C_veg	1960	2000	316.57	368.23	7	–	16	–	0.45	–
NEP	iCO_2	Pretzsch *et al*. (1997)	C_veg	Inventory	*Picea abies*	C_veg	1960	2000	316.57	368.23	6	–	16	–	0.39	–
NEP	eCO_2	Terrer *et al*. (2019)	C_veg	FACE meta-analysis, upscaled	Global	C_veg	–	–	375	625	12	6	67	5.8	0.22	0.11
NEP	eCO_2	Evans *et al*. (2014)	C_veg_abg	FACE NDFF	Desert	–	–	–	375	513	–13	30	37	5.6	–0.44	1.1
NEP	eCO_2	Baig *et al*. (2015)	C_veg_abg_inc	eCO_2 meta-analysis, factorial studies	Multi-biome	–	–	–	362.5	665	21	11	83	6.1	0.32	0.15
NEP	eCO_2	Evans *et al*. (2014)	C_veg_bg	FACE NDFF	Desert	–	–	–	375	513	–9.4	32	37	5.6	–0.31	1.1
NEP	eCO_2	Baig *et al*. (2015)	C_veg_bg_inc	eCO_2 meta-analysis, factorial studies	Multi-biome	–	–	–	362.5	665	35	18	83	6.1	0.5	0.22
NEP	eCO_2	Baig *et al*. (2015)	C_veg_inc	eCO_2 meta-analysis, open ground studies	Multi-biome	C_veg_inc	–	–	360	550	22	6.2	53	5.9	0.47	0.13
NEP	iCO_2	Pretzsch *et al*. (1997)	C_veg_inc	Inventory	*Fagus sylvatica*	C_veg_inc	1960	2000	316.57	368.23	30	–	16	–	1.7	–
NEP	iCO_2	Pretzsch *et al*. (1997)	C_veg_inc	Inventory	*Picea abies*	C_veg_inc	1960	2000	316.57	368.23	10	–	16	–	0.63	–
NEP	eCO_2	Walker *et al*. (2019)	C_veg_inc	FACE meta-analysis	temperate forest	C_veg_inc	–	–	377	576	29	23	53	5.7	0.6	0.43
NEP	eCO_2	Nie *et al*. (2013)	C_veg_root	eCO_2 meta-analysis	Multi-biome	–	–	–	360	645	29	–	79	–	0.43	–
NEP	eCO_2	Hattenschwiler *et al*. (1997)	C_wood	eCO_2 spring Laiatico	*Quercus ilex*	C_veg	30	–	345	650	16	–	88	–	0.23	–
NEP	eCO_2	Hattenschwiler *et al*. (1997)	C_wood	eCO_2 spring Rapolano	*Quercus ilex*	C_veg	30	–	345	650	28	–	88	–	0.39	–
NEP	iCO_2	Hubau *et al*. (2020)	C_wood	Inventory	Tropical Amazon	C_veg	1983	2014	342.01	396.7	12	–	16	2.2	0.77	–
NEP	iCO_2	Brienen *et al*. (2015)	C_wood_abg	Inventory	Tropical Africa	C_veg	1983	2011	342.01	389.79	7.5	–	14	–	0.55	–

Table 2 (Continued)

Process	eCO_2/iCO_2	Study	Variable	Study type, location	Species, genus, biome	Plotted as	Start year[†]	End year[†]	Ambient/ start CO_2	Elevated/ end CO_2	Variable response ratio	95% CI	CO_2 response ratio	95% CI	β	95% CI
NEP	iCO_2	McMahon *et al*. (2011)	C_wood_abg	Inventory, 100 years	Temperate forest	C_veg	1987	2005	348.17	378.23	18	3.6	8.6	2.1	2	0.59
NEP	iCO_2	McMahon *et al*. (2011)	C_wood_abg	Inventory, 50 years	Temperate forest	C_veg	1987	2005	348.17	378.23	27	5.7	8.6	2.1	2.9	0.87
NEP	iCO_2	Qie *et al*. (2017)	C_wood_abg	Inventory	Borneo, intact plots	C_veg	1985	2010	344.99	387.99	5.8	3.4	12	2.2	0.48	0.28
NEP	iCO_2	Yu *et al*. (2019)	C_wood_abv	Inventory	Boreal	–	2001	2008	369.79	384.15	4.9	–	3.9	–	1.3	–
NEP	iCO_2	Yu *et al*. (2019)	C_wood_abv	Inventory	Panbiome	C_veg	1990	2008	353.2	384.15	7.1	2.4	8.8	2.1	0.82	0.32
NEP	iCO_2	Yu *et al*. (2019)	C_wood_abv	Inventory	Temperate	–	1990	2004	353.2	376.12	0	–	6.5	–	0	–
NEP	iCO_2	Yu *et al*. (2019)	C_wood_abv	Inventory	Tropical	–	1994	2009	357.62	385.81	9	–	7.9	–	1.1	–
NEP	iCO_2	Brienen *et al*. (2015)	C_wood_inc	Inventory	Tropical Amazon	C_veg_inc	1983	2011	342.01	389.79	–68	66	14	2.2	–8.8	16
NEP	iCO_2	Hubau *et al*. (2020)	C_wood_inc	Inventory	Tropical Africa	C_veg_inc	1983	2014	342.01	396.7	130	180	16	2.2	5.6	5.5
NEP	iCO_2	Pan *et al*. (2011)	C_woodnecromass	Inventory, upscaled	Global	C_soil	1990	1999	353.2	367.06	2.5	–	3.9	–	0.64	–
NEP	iCO_2	Fernandez-Martinez *et al*. (2017)	NEP	Flux-tower	Ecosystem	NEP	1992	2013	355.4	394.6	57	24	11	2.1	4.3	1.7
NEP	iCO_2_CO_2att.	Fernandez-Martinez *et al*. (2017)	NEP	Flux-tower, CO_2 attribution	Ecosystem	NEP	1992	2013	355.4	394.6	62	13	11	2.1	4.6	1.1
NEP	iCO_2	Fernandez-Martinez *et al*. (2019)	NEP	Atmospheric CO_2 inversion, CO_2 attribution, method 1	Global	NEP	1995	2014	359.52	396.7	560	51	10	2.1	19	3.7
NEP	iCO_2	Fernandez-Martinez *et al*. (2019)	NEP	Atmospheric CO_2 inversion, CO_2 attribution, method 2	Global	NEP	1995	2014	359.52	396.7	190	19	10	2.1	11	2.2
NEP	iCO_2_CO_2att.	Fernandez-Martinez *et al*. (2019)	NEP	Atmospheric CO_2 inversion, method 1	Global	NEP	1995	2014	359.52	396.7	380	32	10	2.1	16	3.1
NEP	iCO_2_CO_2att.	Fernandez-Martinez *et al*. (2019)	NEP	Atmospheric CO_2 inversion, method 2	Global	NEP	1995	2014	359.52	396.7	190	7.6	10	2.1	11	2.1
NEP	iCO_2	Li *et al*. (2016)	NEP	Carbon budget, data assimilation	Global	NEP	1980	2014	337.85	396.7	380	350	17	2.3	9.8	4.7
NEP	iCO_2	Graven *et al*. (2013)	SCA	Atmospheric CO_2, 45-85 north, 500mb	Northern extra-tropics	NEP	1959	2010	315.66	387.99	58	14	23	2.5	2.2	0.48

abg, aboveground; bg, belowground; gstar, gamma star, photorespiratory compensation point; iCO_2_CO_2att., historical study where the change in a variable caused solely by a change in CO_2 has been attributed; inc, increment; LP, Litter production (includes tree wood mortality when expressed as a mass flux); maom, mineral-associated SOM; NDFF, Nevada desert FACE facility; pom, particulate SOM; RS, remote sensing; Vcmax, maximum rate of carboxylation.

[†]Where < 100 value refers to tree age or age since disturbance.

isotopes combined with models (β_{app} = 1.3 ± 2.3) (Ciais *et al.*, 2012). Satellite-based evapotranspiration combined with an ecosystem WUE model estimated increased GPP over recent decades (β_{app} = 1.1 ± 0.5) (Cheng *et al.*, 2017). Fourteen methods to estimate GPP from satellite-based fAPAR resulted in wide-ranging iCO_2 sensitivities (β_{dir} range: −0.39 ± 0.34 to 1.6 ± 1, mean = 0.52 ± 0.3; 2000–2014) (Sun *et al.*, 2019).

Water-use efficiency, stomatal conductance, and transpiration Experimental evidence also supports increased iWUE in response to eCO_2 (β_{dir} = 1.2 ± 0.4; four sites, seven species) (Ainsworth & Long, 2005). In two FACE experiments (Duke University and Oak Ridge National Laboratory, ORNL), tree-ring $\delta^{13}C$ implies increased iWUE (β_{dir} = 1.4 and 1.3, respectively) (Battipaglia *et al.*, 2013). Tree-ring $\delta^{13}C$ samples from across the globe suggest increased iWUE in many biomes since pre-industrial times in northern boreal gymnosperms (β_{app} = 1.2 ± 2 to 1.5 ± 1.6) (Saurer *et al.*, 2004), tropical forests (β_{app} = 1.0) (van der Sleen *et al.*, 2015), and a wide range of forest biomes (β_{app} = 1.19; Keller *et al.*, 2017). Attribution to iCO_2 also suggests increases in iWUE in European *Pinus* and *Quercus* (β_{dir} = 1.0 ± 0.6 and 0.67 ± 0.9; nine to 14 sites) (Frank *et al.*, 2015). Additional environmental factors have contributed to observed iWUE trends (e.g. drying trends have increased iWUE; Saurer *et al.*, 2014).

$\delta^{13}C$ in atmospheric CO_2 combined with mass-balance modelling suggests a global increase in iWUE since pre-industrial times (β_{app} = 0.94 ± 0.2) (Keeling *et al.*, 2017).

Evidence from Duke and ORNL FACE experiments supports increases in ecosystem-scale plant WUE (annual BP/Transpiration; $\beta_{dir,hist}$ = 0.76 and 1.1, respectively) (De Kauwe *et al.*, 2013). Inferred from eddy-covariance, 'inherent' WUE (vapour pressure deficit (VPD) × GPP/ evapotranspiration (ET)) increased in temperate and boreal forests with notably higher magnitude (β_{app} = 4.72; 21 sites) (Keenan *et al.*, 2013). A follow-up study reduced this estimate (β_{app} = 2.5) (Mastrotheodoros *et al.*, 2017). An eddy-covariance calibrated, canopy-scale model suggested iCO_2 reduced g_s ($\beta_{dir,hist}$ = −0.28 ± 0.09) and increased iWUE ($\beta_{dir,hist}$ = 0.73 ± 0.2) (Ueyama *et al.*, 2020). Satellite-based models (2000–2013) of GPP and ET suggest smaller or decreased WUE (GPP/ET) (β_{app} = −0.49 and 0.28) (Tang *et al.*, 2014; Xue *et al.*, 2015).

Experimental evidence has thoroughly demonstrated reduced leaf-scale g_s in response to eCO_2 ($\beta_{dir,fut}$ = −0.22 ± 0.15) (Medlyn *et al.*, 2001). Averaged across FACE experiments (12 sites, 40 species), eCO_2 reduced g_s ($\beta_{dir,fut}$ = −0.60 ± 0.2) but with substantial variability across functional groups (Ainsworth & Long, 2005) and disturbance history (Donohue *et al.*, 2017). Notably for *Eucalyptus saligna* in whole-tree chambers, canopy-scale iWUE was very tightly constrained ($\beta_{dir,fut}$ = 0.98 ± 0.2), and variability in the A_{net} response controlled the g_s response (Barton *et al.*, 2012).

Across four FACE experiments (Duke, EucFACE, ORNL, Swiss Canopy Crane), transpiration responses were only reduced by eCO_2 at ORNL ($\beta_{dir,fut}$ = −0.54), an ecosystem that is rarely water-limited (Leuzinger & Körner, 2010) (De Kauwe *et al.*, 2013; Gimeno *et al.*, 2018). Airborne remote sensing suggested decreased evapotranspiration with long-term volcanically derived eCO_2 in California (Cawse-Nicholson *et al.*, 2018). Stream-gauge networks indicate global increases in runoff (Gedney *et al.*, 2006), in agreement with reduced g_s over the northern hemisphere extratropics (Knauer *et al.*, 2017). However, decreases in runoff have also been observed (Ukkola *et al.*, 2016; Trancoso *et al.*, 2017) and modest runoff increases across the tropics have been driven by precipitation increases (Yang *et al.*, 2016).

2. Biomass production

Elevated $[CO_2]$ increased BP in four temperate-forest, stand-scale (25–30 m diameter) FACE experiments in the early years ($\beta_{dir,fut}$ = 0.56 ± 0.2) (Norby *et al.*, 2005) and over a full decade ($\beta_{dir,fut}$ = 0.49 ± 0.3) (Walker *et al.*, 2019). These forest ecosystems were in the early phases of secondary succession (initiated 1–13 yr after a major disturbance). In three later-succession forests (*c.* 100 yr old), BP did not respond to eCO_2 (note fine-root BP was often not measured): deciduous broadleaved trees ($\beta_{dir,fut}$ = −0.097 ± 1.0 to 0.55 ± 1.7; 8 yr; Bader *et al.*, 2013), *Picea abies* ($\beta_{dir,fut}$ = −0.30 ± 0.7; 5 yr eCO_2; Klein *et al.*, 2016), and a low-productivity *Eucalyptus* woodland ($\beta_{dir,fut}$ = −0.26 ± 0.6; 4 yr eCO_2; Ellsworth *et al.*, 2017; Jiang *et al.*, 2020).

Elevated $[CO_2]$ consistently decreased specific leaf area ($\beta_{dir,fut}$ = −0.16 ± 0.07) (Ainsworth & Long, 2005), which requires increased leaf BP at a given LAI (De Kauwe *et al.*, 2014). Synthesis of experiments (19 sites) suggests that eCO_2 increased grassland leaf and stem BP ($\beta_{dir,fut}$ = 0.17 ± 0.07) (Hovenden *et al.*, 2019), related to summer water savings and spring water availability (Morgan *et al.*, 2004; Hovenden *et al.*, 2019). Meta-analysis found that eCO_2 increased fine-root BP across experiments ($\beta_{dir,fut}$ = 0.56), in forests ($\beta_{dir,fut}$ = 0.92), and, to a lesser degree, in grasslands ($\beta_{dir,fut}$ = 0.18) (Nowak *et al.*, 2004).

Tree-ring analysis at CO_2 springs in Italy (two sites) suggests that eCO_2 increased *Quercus ilex* tree-ring width (a proxy for wood BP) initially (β_{app} = 0.49–0.81), and the increase diminished as trees aged (Hättenschwiler *et al.*, 1997). Basal-area increment (BAI) analysis showed the eCO_2 response stabilized at around 10 yr (β_{app} = 0.27) (Norby *et al.*, 1999).

A large number of tree-ring studies have found little evidence for increases in wood BP. No detectable trends in BAI were found across tropical forests (3 sites, 12 species) (van der Sleen *et al.*, 2015), and both increasing and decreasing trends were found across North American boreal forests (598 sites, 19 species) (Girardin *et al.*, 2016). Syntheses across biomes found no significant increase in tree-ring width since 1950 (β_{app} = 0.23 ± 0.8; 40 sites) (Peñuelas *et al.*, 2011) and variable responses of BAI (β_{app} =-0.45 ± 0.7; 37 sites, 22 species) (Silva & Anand, 2013). Conversely, *Pinus* and *Quercus* tree rings from Missouri showed a positive response to iCO_2 that diminished with tree age (β_{app} =-3.3, at age 1 yr; β_{app} = 1.1, at age 50 yr) (Voelker *et al.*, 2006).

Evidence from multi-plot inventory data consistently show increasing wood biomass (Section III.5), but few of these studies quantify wood BP. A single census interval of eastern-US Forest Inventory Analysis plots (20 000) suggested very little change in wood BP (Caspersen, 2000), but with high uncertainty (Joos *et al.*, 2002). Two large tropical-forest plots showed no change in above-ground wood BP (Clark *et al.*, 2010; Rutishauser *et al.*, 2020). By contrast, tropical forest-plot networks (321 and 244) suggest that above-ground wood BP increased in Amazonia ($\beta_{app} = 1.2 \pm 0.6$) (Brienen *et al.*, 2015) and Africa ($\beta_{app} = 0.69 \pm 0.63$) with a regression-attributed iCO_2 response ($\beta_{app} = 0.54 \pm 1$) (Hubau *et al.*, 2020). Analysis of worldwide forest plots (695) suggested that wood BP increased ($\beta_{app} = 0.94 \pm 1.1$) over recent decades (Yu *et al.*, 2019).

BP–nutrient interactions and progressive nitrogen limitation At Duke FACE, nitrogen availability influenced the magnitude of BP responses (McCarthy *et al.*, 2010) and experiments in later-succession systems with no BP response were limited by nitrogen (Flakaliden; Sigurdsson *et al.*, 2013) and phosphorus (EucFACE; Ellsworth *et al.*, 2017). Limiting factors were not examined for a number of the other later-succession experiments (Bader *et al.*, 2013; Klein *et al.*, 2016).

Elevated [CO_2] experiments in early-succession ecosystems suggested that BP gains were supported by increased nitrogen acquisition rather than changes in stoichiometry (Finzi *et al.*, 2007; Zaehle *et al.*, 2014). Nitrogen acquisition was increased through increased fine-root BP (see earlier), changing root traits (Iversen, 2010; Nie *et al.*, 2013; Beidler *et al.*, 2015), and below-ground carbon flux to mycorrhizal symbionts and rhizosphere microbial associations (Section III.4; Drake *et al.*, 2011; Phillips *et al.*, 2011; Terrer *et al.*, 2018). Meta-analysis suggests that eCO_2 increased nitrogen fixation in more intensively manipulated experiments but not in more natural settings (total 441 studies, rates were scaled to plant or ground-area units; B.A. Hungate, unpublished).

Experimental evidence for progressive nitrogen limitation is limited to a single forest (ORNL; Norby *et al.*, 2010) and a single grassland (Biocon; Reich *et al.*, 2006). Palaeoclimatic evidence suggests that despite increasing carbon storage the nitrogen cycle became more open between the Last Glacial Maximum and the industrial revolution (Fischer *et al.*, 2019; Jeltsch-Thömmes *et al.*, 2019).

Leaf area, water, and land cover interactions In some low LAI ecosystems, eCO_2 increased LAI, but did not in higher LAI (*c.* 5) ecosystems (Norby & Zak, 2011; Bader *et al.*, 2013). However, low LAI (*c.* 1) at EucFACE did not respond to eCO_2 (Duursma *et al.*, 2016). The LAI response to eCO_2 in low LAI systems has been interpreted as CO_2 accelerating open canopies towards closure (Körner, 2006). However, evidence from two FACE sites (Duke and Rhinelander) suggests that LAI can be higher at canopy closure (Walker *et al.*, 2019). Higher above-ground biomass in some grasslands (Hovenden *et al.*, 2019) indicates potential LAI increases, although increases in leaf mass per unit area would reduce the LAI response relative to the biomass response. High grassland biomass responses have been linked to low soil matric potential (Morgan *et al.*, 2004), although more complex interactions with precipitation seasonality have also been indicated (Hovenden *et al.*, 2019).

Satellite data show 'greening' trends over much of the planet, inferred as increasing LAI (Zhu *et al.*, 2016; Mao *et al.*, 2016) and with model-based attribution primarily to iCO_2 (Zhu *et al.*, 2016). Consistent with theory, satellite greenness data suggest increased foliage cover in warm and semiarid regions, probably an iCO_2 effect via increased WUE (Donohue *et al.*, 2013). Tree rings have indicated decreasing sensitivity to rainfall or drought in the eastern US, possibly indicating WUE-mediated iCO_2 response (Wyckoff & Bowers, 2010; Helcoski *et al.*, 2019). However, less severe droughts, noted in the eastern US, probably appear as reduced growth sensitivity (Maxwell *et al.*, 2016). At the Florida scrub oak experiment, eCO_2 alleviated drought-related declines in net ecosystem production (NEP; Li *et al.*, 2007) but the opposite was observed in the Nevada desert FACE (Jasoni *et al.*, 2005).

3. Plant mortality

Glasshouse experiments with potted plants have found little benefit of eCO_2 on survival during drought or high temperature (e.g. Duan *et al.*, 2014; Bachofen *et al.*, 2018). However, remote-sensing evidence shows increased vegetation cover in drylands (Donohue *et al.*, 2013; Section III.2) which suggests a possible reduction in mortality in those regions.

We are unaware of direct or indirect evidence for CO_2-related increases in individual-scale mortality, but growth–mortality relationships provide some insights. Evidence supports both an interspecific growth–survival tradeoff (Wright *et al.*, 2010; Bugmann & Bigler, 2011) and an intraspecific tradeoff (Bigler & Veblen, 2009; Di Filippo *et al.*, 2012, 2015; Büntgen *et al.*, 2019). However, there are common exceptions, with some high-growth-rate species with long life spans (Rüger *et al.*, 2020) and other species that show no, or even negative, growth–mortality relationships (Ireland *et al.*, 2014; Cailleret *et al.*, 2017).

Experimental evidence for stand-scale mortality responses to eCO_2 is rare. In the young, regenerating stand at Rhinelander FACE, over 11 yr of eCO_2 lowered rates of self-thinning (i.e. higher stand basal area for any given stem density; Kubiske *et al.*, 2019).

At broader scales, most inventory networks have shown increases in stand-scale mortality rates. Increases in biomass mortality have been observed in Amazon forests ($\beta_{app} = 2.4$) (Brienen *et al.*, 2015) and across continents ($\beta_{app} = 1.6$–3.9) (Yu *et al.*, 2019). Tree stem mortality rates have increased, across species, elevation, and tree size, in the western US ($\beta_{app} = 6.2 \pm 3$; van Mantgem *et al.*, 2009) and Canada ($\beta_{app} = 6.1$) (Peng *et al.*, 2011). However, none of these studies conclusively attribute trends to iCO_2 and other global change (e.g. temperature) and biotic (e.g. pest and pathogens) agents have often been attributed drivers of mortality trends (Peng *et al.*, 2011; Luo & Chen, 2015). Finally, several networks observed decreases or nonsignificant changes (e.g. in stem mortality rates in Germany (Pretzsch *et al.*, 2014) and biomass mortality in tropical Africa ($\beta_{app} = -0.88 \pm 2$)), although multiple regression estimated that CO_2 increased mortality ($\beta_{dir,hist} = 1.8 \pm 4$) (Hubau *et al.*, 2020).

4. Organic matter decomposition

Evidence for changes in SOM decomposition rates comes primarily from experiments. Many eCO_2 experiments have demonstrated increased plant litter production and allocation of carbon below ground (e.g. Drake *et al.*, 2011; Iversen *et al.*, 2012). Meta-analysis (53 experiments, primarily FACE and OTC) showed that eCO_2 increased litter production ($\beta_{dir,fut} = 0.4 \pm 0.1$) and SOM-decomposition rates ($\beta_{dir,fut} = 0.34 \pm 0.2$) (van Groenigen *et al.*, 2014), yet priming effects are difficult to detect in field studies (van Groenigen *et al.*, 2014; Georgiou *et al.*, 2015).

Results from ecosystem-scale experiments indicate some heterogeneity and nuance in these responses. For example, in a scrub oak ecosystem, 6 yr of eCO_2 increased SOM decay despite unchanged microbial biomass (Carney *et al.*, 2007), and at ORNL FACE a decade of eCO_2 resulted in a small but nonsignificant increase in surface-soil SOM decomposition along with a reduction in microbial nitrogen (Iversen *et al.*, 2012). In a later-succession forest, eCO_2 increased microbial biomass ($\beta_{dir,fut} = 0.40 \pm 0.4$) but with no change in soil respiration ($\beta_{dir,fut} = -0.18 \pm 0.7$) (Bader & Körner, 2010). At EucFACE, +30 ppm eCO_2 increased soil respiration ($\beta_{dir,fut} = 1.3$), but a further increase of 120 ppm produced no additional effect after 3 months ($\beta_{dir,fut} = 0.3$) or 3 yr ($\beta_{dir,fut} = 0.21$) (Drake *et al.*, 2016, 2018). This 3 yr response was nonsignificant but accounted for about half of the additional carbon acquired under eCO_2 (Jiang *et al.*, 2020).

Data on long-term changes in SOM decomposition in response to iCO_2 remain limited. Synthesis of 23 flux towers with increased GPP (Section III.1) suggested a nonsignificant increase in ecosystem respiration (R_e; $\beta_{app} = 0.58 \pm 1$) (Fernández-Martínez *et al.*, 2017). Synthesis and statistical upscaling of chamber measurements suggested that global soil respiration has increased (β_{app} =- 0.22) (Bond-Lamberty & Thomson, 2010). Statistical predictors of this trend include temperature anomaly and year (possibly an iCO_2 effect). Notably, heterotrophic respiration would be expected to increase if C_{soil} increased, even with no change in decomposition rates.

Accelerated SOM-decomposition may release nutrients and feed back onto the activity of plant processes. For example, at Duke FACE, increased root exudation ($\beta_{dir,fut} = 1.1 \pm 0.6$) was coupled with a nonsignificant but substantial increase in microbial biomass ($\beta_{dir,fut} = 1.1 \pm 1.3$) and production of nitrogen-acquiring extracellular enzymes (Phillips *et al.*, 2011). Exoenzyme activity was increased at Duke and Rhinelander FACE (Larson *et al.*, 2002; Finzi *et al.*, 2006), although no change in nitrogen mineralization was observed in laboratory incubations (Zak *et al.*, 2003), perhaps suggesting that stimulation of microbial activity required plant inputs. Conversely, leaf $\delta^{15}N$ suggests that eCO_2 may have increased nitrogen mineralization but not ring width in mature trees in a European forest (Bader *et al.*, 2013). eCO_2 increased nitrogen and phosphorus mineralization for a limited period at EucFACE (Hasegawa *et al.*, 2016) and enzyme activity in an alpine forest (Souza *et al.*, 2017). Conversely, meta-analysis suggests eCO_2 increased fine-root C : N ratios ($\beta_{dir,fut} = 0.13$) (Nie *et al.*, 2013), which are associated with lower decomposability.

Contrasting mycorrhizal associations have been linked to biomass responses under low soil nitrogen conditions (Phillips *et al.*, 2013; Terrer *et al.*, 2016). Ectomycorrhizal (ECM) fungi are assumed capable of stimulating SOM decomposition, while arbuscular mycorrhizal (AM) fungi are not, resulting in increased nitrogen in above-ground BP in ECM trees but not in AM plants, primarily grasses (Terrer *et al.*, 2018). Conversely, AM association with *Avena fatua* in a laboratory and field setting increased SOM-decomposition rates under eCO_2 ($\beta_{dir,fut} = 1.4$) (Cheng *et al.*, 2012).

5. Terrestrial ecosystem carbon

Direct evidence from site-scale studies In the four longest-running FACE experiments eCO_2 over a decade increased C_{veg} increment ($\beta_{dir,fut} = 0.60 \pm 0.4$) in these early-succession temperate forests (Walker *et al.*, 2019). eCO_2 of geological origin increased tree basal area in 30-yr-old trees ($\beta_{dir,fut} = 0.23$–0.39) (Hättenschwiler *et al.*, 1997). Conversely, in the later-succession forest at EucFACE, 4 yr of eCO_2 did not increase C_{veg} increment (Jiang *et al.*, 2020), probably because of phosphorus limitation (Ellsworth *et al.*, 2017). Other experiments in later-succession forests did not quantify C_{veg}. Meta-analysis and extrapolation (138 experiments) predicted a global increase in C_{veg} ($\beta_{dir,fut} = 0.22 \pm 0.1$) related to soil C : N ratio in AM-associated ecosystems and soil phosphorus in ECM-associated ecosystems (Terrer *et al.*, 2019). Biomass responses were generally higher in ECM systems than in AM systems (Terrer *et al.*, 2016), while another meta-analysis showed analogous biomass responses in trees compared with grasses (Song *et al.*, 2019).

Synthesis of meta-analyses found that eCO_2 increased C_{soil} across all (> 200) experiments analysed ($\beta_{dir,fut} = 0.039 \pm 0.03$) but not in field experiments lasting ≥ 2 yr without nitrogen addition (25) ($\beta_{dir,fut} = 0.0054 \pm 0.03$) (Hungate *et al.*, 2009). However, C_{soil} responses to eCO_2 at individual sites are mixed. For example, a decade of eCO_2 increased C_{soil} at ORNL FACE ($\beta_{dir,fut} = 0.51 \pm 0.6$, 0–90 cm) (Iversen *et al.*, 2012) and in a desert ecosystem ($\beta_{dir,fut} = 0.59 \pm 0.62$) (Evans *et al.*, 2014), but not in a scrub oak ecosystem ($\beta_{dir,fut} = -0.15 \pm 0.5$) (Hungate *et al.*, 2013). In the desert ecosystem, inorganic carbonate pools may have contributed to increases in C_{soil} through nocturnal CO_2 uptake (Hamerlynck *et al.*, 2013) although net effects are probably small (Soper *et al.*, 2017).

Given limited data, litter addition experiments can also provide some insights. Synthesis of priming responses to litter addition (26 studies) suggested that 32% of litter inputs accumulate as C_{soil} (Liang *et al.*, 2018). Ten to 30 yr of doubled above-ground litter inputs in temperate forests increased C_{soil} at two sites (29 ± 13% and 33 ± 28%) but had no effect at three sites (Lajtha *et al.*, 2018), or in one tropical forest (Sayer *et al.*, 2019). Based on these responses and assuming that doubled CO_2 doubles litter production (which is unlikely), $\beta_{dir,hist}$ for C_{soil} would range from 0 to 0.41 ± 0.3.

Measurement of NEP requires whole-ecosystem enclosure, and thus data are few. In a US salt marsh, higher rates of NEP were sustained over 19 yr in both C_3 and C_4 communities (Drake, 2014). A data-assimilation approach provided a comprehensive carbon budget at EucFACE showing no change in C_{eco} (Jiang *et al.*, 2020).

Indirect evidence from global and regional studies Spatially explicit atmospheric $[CO_2]$ measurements, fossil-fuel emissions, and other data are integrated using atmospheric transport models to infer terrestrial net biome production (NBP). These 'inversions' suggest a global NBP of 2.3 ± 0.9 (MACC-II), 2.3 ± 1.5 (Jena-CarboScope) (1995–2014; Fernández-Martínez *et al.*, 2019), and 1.9 ± 0.5 PgC y^{-1} (2010–2014; Li *et al.*, 2018) and all estimated positive trends in global NBP (β_{app} = 19 ± 7, 11 ± 4, 9.8 ± 5). These estimates of NBP include both 'natural' NBP and land-use change-related (instantaneous and legacy) NBP.

Global land-use change-related NBP was estimated from bookkeeping models at −1.4 ± 1.4 Pg C yr^{-1} (2000–2009; Friedlingstein *et al.*, 2019), and are predominantly in the tropics (−1.4 ± 0.3 Pg C yr^{-1}) with fluxes outside the tropics balancing to a net flux of near zero (Houghton & Nassikas, 2017). Regional analysis of NBP show a strong sink in northern hemisphere extra-tropics (2.3 ± 0.6 Pg C yr^{-1} (1992–1996), 2.2 ± 0.5 Pg C yr^{-1} (2001–2004)) but a substantial source in the tropics (−1.1 ± 1.5 (1992–1996) and −0.9 ± 0.9 PgC yr^{-1} (2001–2004)) (Gurney *et al.*, 2004; Peylin *et al.*, 2013). Combined with land-use change-related NBP, these inversion results suggest small 'natural' NBP in the tropics (*c.* 0.3–0.5). However, analysis of the vertical atmospheric $[CO_2]$ gradient suggested close-to-neutral tropical NBP (Stephens *et al.*, 2007), implying 'natural' NBP of similar magnitude and opposite sign to land-use change-related NBP, attributed primarily to iCO_2 (Schimel *et al.*, 2015).

Flask, aircraft, and satellite-based measurements show trends in the seasonal-cycle amplitude of $[CO_2]$ since *c.* 1960 (Keeling *et al.*, 1996; Graven *et al.*, 2013; Yin *et al.*, 2018), implying seasonal intensification of northern NBP (β_{app} = 2.2 ± 0.6) (Graven *et al.*, 2013). iCO_2 has been implicated as a major driver of these trends (Forkel *et al.*, 2016; Bastos *et al.*, 2019), although increasing crop production (Gray *et al.*, 2014; Zeng *et al.*, 2014) and warming-induced increasing vegetation cover (Keenan & Riley, 2018) are also likely candidates.

Carbon budgeting estimated global 'natural' NBP at 3.6 ± 1.0 Pg C yr^{-1} (2009–2018) and 141 Pg C since 1959 from the budget residual, and 3.2 ± 1.2 Pg C yr^{-1} and 130 Pg C from process-based models (Friedlingstein *et al.*, 2019). Based on the residual estimate of 'natural' NBP and the lower and upper bounds of either global vegetation or global ecosystem carbon stocks, β_{app} = 0.93–1.4 (assuming all the sink is in vegetation) or β_{app} = 0.18–0.29 for ecosystem carbon (global vegetation and nonpermafrost soils).

Synthesis and extrapolation of global inventory data suggested increased C_{eco} (β_{app} = 1.0 ± 0.6), C_{veg} (β_{app} = 1.9), C_{soil} (β_{app} = 0.31), litter carbon (β_{app} = 0.92), and dead wood carbon (β_{app} = 0.64) (Pan *et al.*, 2011). Few additional data on C_{soil} changes over the historical period are available. Evidence from multiplot forest-inventory data consistently shows net gains in wood C_{veg} in recent decades in tropical Africa (β_{app} = 0.77; Hubau *et al.*, 2020), the Amazon (β_{app} = 0.69; Brienen *et al.*, 2015), Borneo (β_{app} = 0.48 ± 0.3; Qie *et al.*, 2017), and in large 50 ha plots across the tropics (β_{app} = 0.30 ± 0.24; Chave *et al.*, 2008). Wood C_{veg} also increased in plots across the eastern US (β_{app} = 2.9 ± 1.5; McMahon *et al.*, 2010) and globally (β_{app} = 0.82 ± 0.5; Yu *et al.*, 2019). Long-term geological CO_2 release was associated with reduced lidar-estimated above-ground C_{veg} (Cawse-Nicholson *et al.*, 2018).

Flux towers measure NEP directly, yet have been running for a relatively short time. Synthesis of 23 flux towers indicate increased NEP (β_{app} = 4.3 ± 2), with high CO_2 sensitivity ($\beta_{dir,hist}$ = 4.6 ± 2) (Fernández-Martínez *et al.*, 2017).

IV. Synthesis

1. Evidence for the CO_2-fertilization hypothesis

In this section we integrate and interpret the evidence for change in the components of the carbon cycle during the historical record concurrent with increasing $[CO_2]$ (iCO_2; *c.* 280–400 ppm), in response to elevated $[CO_2]$ (eCO_2; *c.* 390–500 ppm), and the probability and magnitude of iCO_2 as a driving factor in the historical change. In doing so we acknowledge that we are mixing evidence across scales, measurements, methods of analysis, and, in some cases, different variables that may not be perfectly comparable. However, this is required for a broad synthesis, and a formal meta-analysis is not our intention. We assign confidence as 'high' (all estimates agree), 'medium' (estimate means disagree, substantial overlap in confidence intervals), or 'low' (estimate means disagree, little overlap in confidence intervals).

Physiology A number of independent lines of indirect evidence – ice-core OCS (Campbell *et al.*, 2017) and O^{18} (Ciais *et al.*, 2012), glucose isotopomers (Ehlers *et al.*, 2015), satellite ET (Cheng *et al.*, 2017), and flux-partitioned eddy-covariance (Fernández-Martínez*et al.*, 2017) – provide high confidence that terrestrial GPP has increased concurrently with iCO_2. Estimates of the GPP increase disagree by a factor of 1.7 (β_{app} = 0.95–1.6, mean = 1.2; Table 2), but overlap in confidence intervals (Figs 3, S2) indicates that these estimates are consistent and suggests medium confidence in the magnitude of the increase in GPP concurrent with iCO_2. Above the canopy-scale GPP can be measured only indirectly, and most of these estimates are a function of the $[CO_2]$ trend (Box 3; isotopomers, satellite, OCS) which introduces a circularity. However, we place less confidence in estimates (usually satellite-based) that omit a CO_2 effect from the theory used in their GPP estimation (Box 3; De Kauwe *et al.*, 2016). Flux-partitioned eddy-covariance provides the only estimate of GPP that does not require $[CO_2]$ in its calculation and provides the highest β_{app} of 1.6 ± 0.9 (Fernández-Martínez *et al.*, 2017). A smaller proportion of this change was attributed to iCO_2 ($\beta_{dir,hist}$ = 1.2 ± 0.6).

Synthesis of direct evidence from experiments provides high confidence that ecosystem-scale eCO_2 increases diurnal photosynthesis in leaves ($\beta_{dir,fut}$ = 0.68 ± 0.2). This increase is very similar to the theoretical value for a light-saturated leaf ($\beta_{dir,fut}$ = 0.70 ± 0.2, Table S1). The theoretical value for the canopy-scale photosynthesis response to iCO_2 (280–410 ppm,

$\beta_{dir,fut}$ = 0.60 ± 0.3; Table S1) is about half the observed mean increase in GPP concurrent with iCO_2 ($\beta_{dir,hist}$ = 1.2). For iCO_2 to be the sole driver of the observed responses all leaves would have to be operating at the light-saturated rate of increase and there would have to be additional positive feedbacks of equivalent magnitude.

The majority of global models tend to follow the theoretical response to iCO_2 (Keenan *et al.*, 2016). A carbon cycle model was able to replicate the OCS increase in GPP (β_{app} = 0.95 ± 0.2) and change in northern seasonal [CO_2] amplitude by hypothesizing leaf optimization and predicting a substantial increase in LAI (note the phosphorus cycle was disabled) (Haverd *et al.*, 2020). However, it is not clear that leaves optimize as hypothesized (Smith & Keenan, 2020), and models consistently represent allocation and LAI simplistically. For example, LAI trends are inferred in high-LAI tropical rainforests (Zhu *et al.*, 2016). In these regions models are probably predicting an increase in maximum LAI, which conflicts with experimental evidence and resource investment theory. An alternative hypothesis is that iCO_2 accelerates the recovery of forest gaps such that landscape-scale LAI is greater – a hypothesis not represented by any of the models used for attribution. Outside of tropical forests, changes in LAI are related to both iCO_2 (Donohue *et al.*, 2013) and temperature-stimulated increases in growing season length (Keenan & Riley, 2018). An additional consideration is that models tend to underestimate GPP relative to solar-induced fluorescence (a GPP proxy) in agricultural regions (Guanter *et al.*, 2014; Walker *et al.*, 2017), agriculture being another major factor of global change. Taken together, we are confident that the historical GPP increase was primarily driven by iCO_2 and also that iCO_2 was not the sole driving factor. However, it is unclear which factors might be driving the additional change in GPP.

A number of independent lines of indirect evidence – tree-ring $\delta^{13}C$ (e.g. Saurer *et al.*, 2004; Peñuelas *et al.*, 2011; Frank *et al.*, 2015), flux-partitioned eddy-covariance (Keenan *et al.*, 2013; Mastrotheodorus *et al.*, 2017), and atmospheric $\delta^{13}C$ (Keeling *et al.*, 2017) – provide high confidence that iWUE (across leaf to global scales) and WUE (across leaf to ecosystem scales) have increased over the historical period (β_{app} = 0.85–3.9, mean = 1.5). There remain large differences (factor of 5) between these estimates of the increase, primarily as a result of the eddy-covariance estimates (β_{app} = 2.4 ± 2.0 and 3.9 ± 2.5). The causes for these differences are not fully understood, although scale (Medlyn *et al.*, 2017), plasticity (Mastrotheodorus *et al.*, 2017), high variability and short timescales (indicated by the high uncertainty), and GPP trends that are higher than expected from iCO_2 alone (see earlier) all play a role. Eddy covariance estimates skew the mean and the modal change is around β_{app} = 1 (Fig. 3), similar to the mean for iCO_2-attribution studies ($\beta_{dir,hist}$ = 0.80) and the theoretical value for iWUE ($\beta_{dir,hist}$ = 1.1). As with GPP, other than eddy covariance these indirect methods use [CO_2] in their calculation (Box 3). Satellite estimates of WUE suffer from very short time periods (13 yr) with low signal-to-noise ratio, leaving little confidence in these trend estimates. Direct evidence from multiple experiments support iWUE and WUE increases ($\beta_{dir,fut}$ = 0.65–1.6, mean = 1.1) in agreement with predictions from theory (Fig. 2). Taken together this evidence provides high confidence that iCO_2 has increased iWUE, medium confidence that the magnitude is in accordance with theory, and low confidence in the magnitude of the historical change in WUE.

How do these changes in iWUE translate to changes in water use? Theory predicts that iWUE (A_{net}/g_s) responses are very tightly constrained ($\beta_{dir} \approx 1$), so if the change in A_{net} is below 1, g_s will decrease (Barton *et al.*, 2012). The observed changes in GPP ($\beta_{app} \approx$ 1) suggest that widespread and broad-scale reductions in g_s might not have occurred. Reductions in stomatal conductance could occur at points in time or space, but as spatial and temporal scale increases, iCO_2-induced decreases in stomatal conductance probably translate into smaller decreases in transpiration (Field *et al.*, 1995; Körner *et al.*, 2007).

Increased vegetation cover in semiarid regions (Donohue *et al.*, 2013; Ukkola *et al.*, 2016), increased rooting depth (Y. Yang *et al.*, unpublished; Iversen, 2010), soil–water feedback on g_s, competition and atmospheric coupling (Jarvis & McNaughton, 1986; Buckley *et al.*, 2017; Sperry *et al.*, 2019; Sabot *et al.*, 2020) are all mechanisms that may lead to no change in water use at larger scales. This is particularly likely to be the case in water-limited regions where long-term transpiration is primarily precipitation-driven (Fatichi *et al.*, 2016), that is, plants use the water that is available.

Biomass production Ecosystem-scale forest-inventory networks suggest increases in wood BP concurrent with iCO_2 (mean $\beta_{app} \approx 1$; Brienen *et al.*, 2015; Yu *et al.*, 2019, Hubau *et al.*, 2020). Conversely, evidence from tree rings is mixed (e.g. Peñuelas *et al.*, 2011; Silva & Anand, 2013). Both of these methods are subject to potential sampling biases (Box 3). However, the tree-ring biases are potentially larger and can be either positive (Nehbas-Ahles *et al.*, 2014) or negative (Brienen *et al.*, 2016). The inventory evidence provides medium confidence in an increase in wood BP over the historical period, with low confidence in the magnitude (β_{app} c. 1). However, this is an area of disagreement among several in our authorship group.

Many studies show increased BP in response to eCO_2 (e.g. Baig *et al.*, 2015), but these studies are often short-lived and under artificial conditions. Evidence from long-term, large-scale FACE experiments (< 10 experiments) is mixed, with both increases (e.g. Norby *et al.*, 2005) and no change in BP observed (e.g. Bader *et al.*, 2013; Jiang *et al.*, 2020) ($\beta_{dir,fut}$ = − 0.3 to 0.56, mean = 0.19). Many studies show a BP response to eCO_2 that is higher at sites with higher nutrient availability (e.g. Terrer *et al.*, 2018), greater when nutrients were added (e.g. Reich *et al.*, 2006; Sigurdsson *et al.*, 2013), or show no response when nutrients are low (e.g. Sigurdsson *et al.*, 2013; Ellsworth *et al.*, 2017). However, strong evidence for the widely held progressive nitrogen limitation hypothesis is restricted to two experiments (Biocon, ORNL) (Reich *et al.*, 2006; Norby *et al.*, 2010). At both of these experiments nutrient dynamics also caused declining BP in the ambient treatments, indicating that eCO_2 responses can be tied, via nutrient availability, to underlying ecosystem dynamics.

Biomass production responses were observed in earlier-succession more-disturbed ecosystems, which also tend to have higher nutrient availability (Körner, 2006). The experiments with no response were often situated in later-succession forests, some of

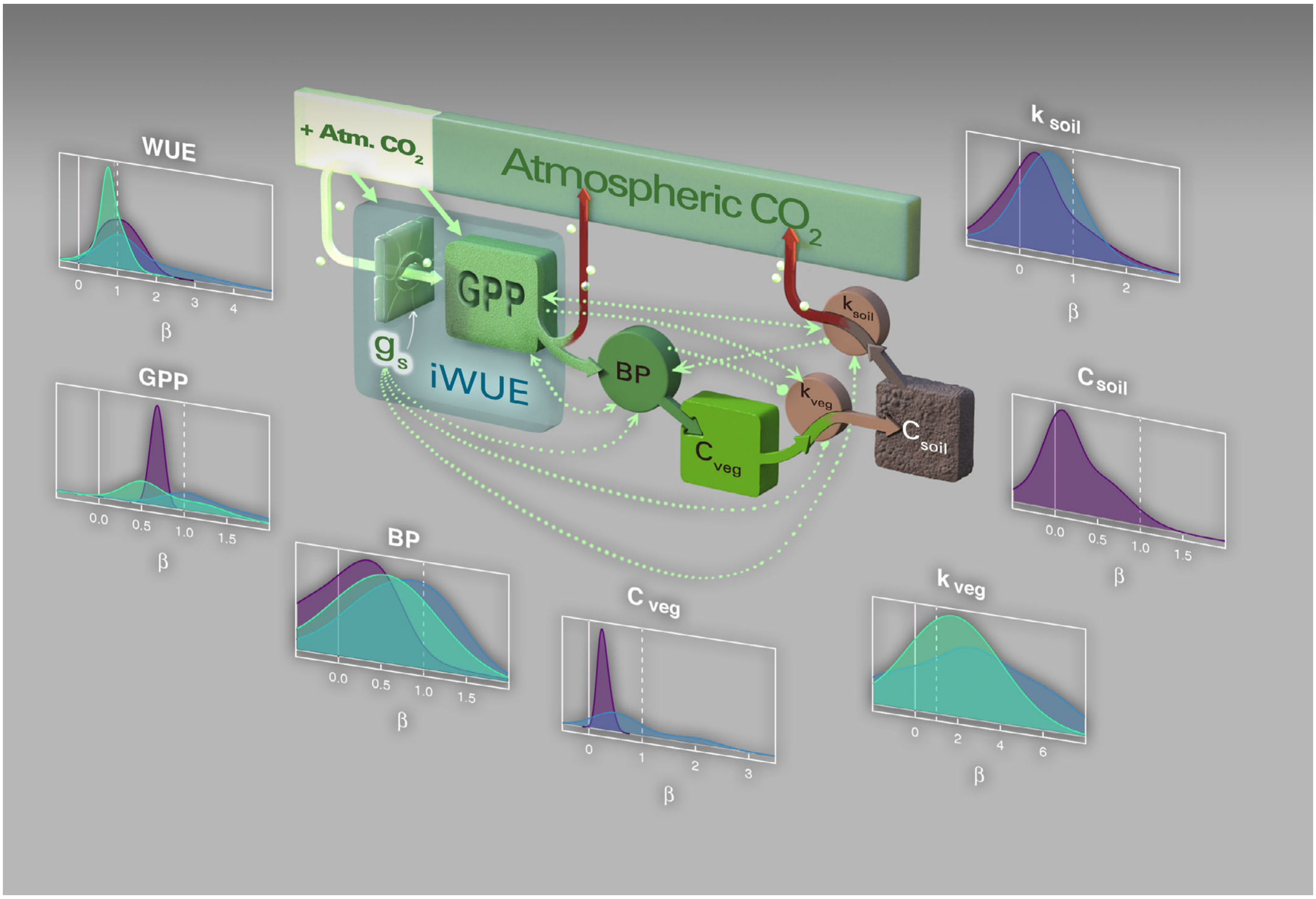

Fig. 3 β distributions based on data from Table 2 for water-use efficiency (WUE), gross primary production (GPP), biomass production (BP), turnover rate of vegetation (k_{veg}) and soil organic matter (k_{soil}), and plant (C_{veg}) and soil (C_{soil}) carbon. Data are organized by CO_2 response category – increasing [CO_2] (iCO_2, blue), attribution to iCO_2 (green), and elevated [CO_2] (eCO_2, purple). See Supporting Information Figs S2–S4 for further details.

which were also severely limited by nutrients. The forest inventories in which BP increases concurrently with iCO_2 were observed in later-succession, primarily tropical, forests that are assumed to be strongly nutrient-limited. These inventory responses are high ($\beta_{app} \approx 1$) compared with the results from experiments even in earlier-succession forests ($\beta_{dir,fut} = 0.49 \pm 0.3$). However, the evidence is insufficient to robustly evaluate how eCO_2 affects late-successional and tropical forests. Taken together, this evidence suggests high confidence that eCO_2 can stimulate BP ($\beta_{dir,fut} \approx 0.5$), that the response is diminished by nutrient limitations, and that the observed inventory response is probably a result of iCO_2 and additional factors.

Vegetation mortality A number of independent plot networks provide high confidence that tree mortality has increased over the historical period but low confidence in the magnitude ($\beta_{app} = -1.2$–7.4, mean = 2.8; Figs 3, S3). The greatest changes are primarily attributed to drought. Causes of mortality are often stochastic, multifactorial, and play out over long time periods, making trend identification and attribution at ecosystem and landscape scales uncertain (McMahon *et al.*, 2019). For individual scale mortality, an intraspecific growth–survival tradeoff is apparent for some species (e.g. Di Fillipo *et al.*, 2015), which would reduce life spans if iCO_2 increases wood BP. However an intraspecific growth–survival tradeoff is not ubiquitous among species (e.g. Cailleret *et al.*, 2017).

Glasshouse eCO_2 experiments suggest that eCO_2 does not reduce drought-related mortality (e.g. Duan *et al.*, 2014; Bachofen *et al.*, 2018). However, eCO_2 commonly increased leaf area in these experiments, increasing transpiration which probably exacerbated mortality risk (Duan *et al.*, 2018). What does this mean for eCO_2 responses in ecosystems? Owing to the juvenile growth stage of these plants, leaf area increases were much higher than expected in closed canopy systems (see Box 3), and increased root BP from eCO_2 would exacerbate pot-volume constraints on root proliferation. Inference from these experiments is limited. At the stand scale there is very limited evidence that eCO_2 might change self-thinning relationships allowing higher basal area for a given stem density (Kubiske *et al.*, 2019). Evidence for changes in mortality caused by iCO_2 is weak and mostly indirect with limited support for both increases and decreases in individual and stand-scale mortality rates. Taken together the response of mortality to iCO_2 and eCO_2 is unknown, even the direction of change is unclear.

Organic matter decomposition The few studies of soil or ecosystem respiration show small (β_{app} = 0.22; Bond-Lamberty & Thompson, 2010) or nonsignificant increases (β_{app} = 0.58 ± 1; Fernández-Martínez *et al.*, 2017). These trends could possibly be related to increasing heterotrophic respiration and decomposition, but increasing temperature is inferred as the cause, not iCO_2 (e.g. Bond-Lamberty *et al.*, 2018). Owing to the low number of studies, there is low confidence that SOM decomposition has increased over the historical period and it is unknown whether SOM decomposition rates have increased.

Evidence from eCO_2 experiments generally supports the theory that rising [CO_2] increases SOM-decomposition rates (e.g. van Greonigen *et al.*, 2015) as a result of increases in microbial biomass, rhizosphere priming, mycorrhizal association and increases in soil water content (see references in Section III.4). Smaller changes in decomposition rates have been associated with lower microbial biomass and higher soil water (Bader & Körner, 2010; Iversen *et al.*, 2012). Taken together, the evidence suggests there is medium confidence that eCO_2 increases rates of SOM decomposition but with low confidence in the magnitude. Increasing SOM decomposition will also release nutrients that may be available for plant growth and BP. Plant nutrient acquisition through mycorrhizal and other root–microbe interactions are probably mediators of this process (Terrer *et al.*, 2018). Notably, the large step-change in eCO_2 experiments compared with the more gradual iCO_2 could lead to a greater imbalance of available resources resulting in a carbon surplus (Box 3) which could fuel greater microbial activity. It is worth noting that increased SOM-decomposition rates do not necessarily imply lower C_{soil} if litter inputs are also increasing (Liang *et al.*, 2018).

Terrestrial ecosystem carbon Multiple independent lines of evidence – global-scale carbon budgeting (Friedlingstein *et al.*, 2019), atmospheric inversions (e.g. Peylin *et al.*, 2016; Fernández-Martínez *et al.*, 2019), seasonal [CO_2] amplitude trends (Graven *et al.*, 2013), and forest inventories (e.g. Pan *et al.*, 2011; Hubau *et al.*, 2020) – imply a CO_2 sink in terrestrial ecosystems (Figs 3, S4). This evidence provides high confidence that terrestrial ecosystem carbon has increased over the historical period, with substantial changes in the 'natural' carbon sink almost balanced by a net carbon source from land-use change. Global carbon budgeting and global forest analysis suggest responses concurrent with iCO_2 in the range, β_{app} = 0.18–1.0. The 'natural' carbon store response estimated for global intact forests (β_{app} = 0.66 ± 0.4; Pan *et al.*, 2011) is higher than estimated for the 'natural' land surface (β_{app} = 0.18–0.29; Friedlingstein *et al.*, 2019). Trends observed in eddy-covariance NEP (site-scale 'natural' sink) and inversion NBP (global-scale combined 'natural' and land-use sink) are extremely high (β_{app} = 4.3–19, mean 11). The extremely high β_{app} for global NBP (and, to a lesser degree, NEP) results from global NBP being near zero as the 'natural' sink is almost balanced by the net source from land-use change, and thus small absolute changes can be high in relative terms (Box 3).

CO_2 effects on terrestrial carbon are convolved with the effects of concurrent anthropogenic changes in climate, nitrogen deposition, and land-use change, including agricultural intensification and fire management. Attribution analyses indicate a primary role for iCO_2 (e.g. Schimel *et al.*, 2015; Keenan *et al.*, 2016; Bastos *et al.*, 2019; Fernández-Martínez *et al.*, 2019; Haverd *et al.*, 2020). These analyses depend on the inclusion of accurate explanatory-variable datasets and accurate process representation in models, which may not be the case. Quantification of the effect of iCO_2 on global carbon storage in terrestrial ecosystems remains elusive.

As with BP responses, studies of forest inventories show higher C_{veg} responses (β_{app} = 0.3–2, mean = 0.85) than studies of eCO_2 experiments (β_{app} = 0.22–0.39) (Fig. 3). However, the highest values come from two analyses: one that includes global forest regrowth (β_{app} = 1.9; Pan *et al.*, 2011) and younger (*c.* 50–100 yr old) temperate forests (β_{app} = 2 ± 1; McMahon *et al.*, 2011). Exclusion of these higher change studies results in a narrower range (β_{app} = 0.3–0.85, mean = 0.57). This exclusion narrows the difference between responses inferred from iCO_2 and eCO_2 studies, which is consistent with theory as relative stock changes are underestimated more in short-term experiments than in inventory-type studies (Fig. S2). Responses of vegetation carbon increment may give a more accurate estimate of responses in systems that are far from equilibrium when initially exposed to eCO_2 (Fig. S2). Vegetation carbon increment responses estimated from FACE experiments (β_{app} = 0.60 ± 0.4; Walker *et al.*, 2019) are consistent with the reduced range from inventory studies. However, the theoretical underestimation of undisturbed forest-inventory responses (Fig. S2) yet similarity of these responses with those from disturbed forests subjected to eCO_2 and not the lower values from undisturbed forests (e.g. Jiang *et al.*, 2020) requires further consideration. Either eCO_2 experiments are underestimating responses or other factors have affected the inventory evidence. Both of these evidence types are likely to be missing the full extent of mortality (e.g. Chambers *et al.*, 2013), and evidence from larger-scale 50 ha plots suggests a lower response for intact tropical forests (β_{app} = 0.30 ± 0.2; Chave *et al.*, 2008).

Evidence of changes in C_{soil} is mixed and context-dependent. On average there is no detectable response across experiments (Hungate *et al.*, 2009), although at some individual sites, C_{soil} did accumulate (e.g. Iversen *et al.*, 2012; Evans *et al.*, 2014). The only study (to our knowledge) of soil carbon changes concurrent with iCO_2 suggests a relative response in global forests (β_{app} = 0.31; Pan *et al.*, 2011), which would be substantial if extrapolated to mineral soils globally. As with vegetation carbon stocks, the long-term, relative responses of soil carbon stocks are probably underestimated by short-term eCO_2 experiments (Fig. S2). Taken together, evidence suggests medium confidence that eCO_2 increases ecosystem carbon stocks over short to medium timescales and that iCO_2 has contributed to the change over the historical period, but with low confidence in the magnitude.

2. What we need to know

Confidence in the magnitude of CO_2 effects is generally low. In particular, iCO_2 attribution is a major challenge in testing the CO_2-fertilization hypothesis over the historical period. Attribution often relies on empirical regression that simply indicates correlation; anything with a trend over the historical period will be correlated with iCO_2. We advocate using log-log β as a stable (Notes S1; Fig. S1), relativized metric for comparison with theoretical expectations and other studies.

Process-based models are also used to deconvolve causation from multiple global-change factors. Models often represent key mechanisms oversimplistically and yet are also equifinal, while model ensembles represent a nonrandom sample of nonindependent models (Beven, 2006; Fatichi *et al.*, 2019; Sanderson & Fisher, 2020). Thus, models need always to be interpreted in the context of the mechanisms they represent, those they do not, how representations might bias results, and how well they reproduce observations (e.g. Medlyn *et al.*, 2015). Mechanistic models (or modules) of BP, resource acquisition and allocation, how soil and plant water status affect g_s, plant–microbe effects on soil decomposition, vegetation structure and demography (e.g. competition, mortality), and land-use need to be developed and applied more extensively to the CO_2-fertilization hypothesis. Alternative hypotheses to explain observed phenomena should be evaluated within model ensembles, and calibrated to allow the hypotheses to compete on an equal footing (e.g. Zhang *et al.*, 2015). Agile and extensible models (e.g. Clark *et al.*, 2015; Walker *et al.*, 2018) will be needed to rapidly incorporate this understanding, including uncertainty, into the internally consistent and quantitative systems-level theory that models represent.

It is crucial that future eCO_2 experiments are designed and resourced to understand the mechanistic basis for responses (or lack thereof) and do not simply report significance or effect sizes. Integration with extensible, process-based models will help us to evaluate and explore the mechanistic basis for observed responses (Medlyn *et al.*, 2015). During the lifetime of long-term experiments, new hypotheses will arise to explain unexpected or key observations that may help to provide context and mechanisms underlying the observed responses. These long-term experiments represent very large investments, and for relatively small additional investment, related studies can test mechanistic hypotheses as they arise during an experiment's lifetime.

3. Suggestions for high-priority future studies

- *Understanding the mechanistic basis for GPP increases observed over the historical period and how this relates to water use.* GPP, iWUE, and water use are intimately tied. The mechanisms by which plants might adjust to iCO_2 (photosynthetic acclimation/optimization, more and deeper roots, g_s responses to water status) are not fully understood and thus not well explored within models. A quantitative synthesis of canopy or stand-scale photosynthetic responses in eCO_2 experiments would be informative.
- *Biomass production* inferred from tree rings and forest inventories reach very different conclusions. Where possible, studies that can integrate these two types of evidence, such as tree-ring sampling at inventory sites (e.g. Dye *et al.*, 2016; Evans *et al.*, 2017), acknowledging respective biases, will be fruitful. The mechanisms underlying how increased GPP leads to increased BP and increased nutrient acquisition through plant–microbe associations are key areas for future study, especially over successional gradients. eCO_2 studies in mid- and late-succession ecosystems, and tropical, boreal, semiarid, and savannah ecosystems will help to address the young, temperate ecosystem bias in eCO_2 studies.
- *How iCO_2 affects mortality* is key to understanding C_{veg} and community responses to iCO_2. As mortality is a relatively rare event in established vegetation, change detection and attribution of causation require large-scale, long-term monitoring and, ideally, experiments (Hartmann *et al.*, 2018). Understanding the mechanics of observed growth–mortality tradeoffs and whether iCO_2 may be alleviating mortality in semiarid regions is a high priority.
- *Studies of the C_{soil} decomposition rate* over the historical period are practically nonexistent; additional studies are required. As with BP, efforts to fully understand plant–microbe–soil (and probably invertebrate), carbon–nutrient interactions continue to be a high priority. Furthermore, investigation of responses in deep soil layers are few or nonexistent. Understanding how the opposing processes of increased litter production, root–microbe interactions, increased decomposition rates, and rates of mineral-associated SOM formation balance to affect C_{soil} throughout the soil profile will be key to predictive understanding. This may be especially relevant in nonforest ecosystems, where the largest potential change in carbon storage is below ground.
- *iCO_2 affects ecosystem carbon primarily through effects on NEP, and thus understanding of C_{eco}* responses to iCO_2 will emerge from these research priorities. Further, NBP is what the atmosphere 'sees', which includes additional nonrespiratory carbon losses caused by fire (anthropogenic and wild), hydrological export, and export of consumer goods. iCO_2 may interact with some nonNEP fluxes (e.g. greater grassland BP, leading to higher fuel loads, greater BP in regrowing forests following land-use change). Land-use change NBP is often calculated without considering iCO_2 and separately from 'natural' NBP caused by iCO_2, climate change, nitrogen deposition, and other factors (e.g. Friedlingstein *et al.*, 2019), although the boundary between these fluxes is blurred (Pongratz *et al.*, 2014). Integrated studies that consider all of these factors, especially land-use change (including iCO_2 acceleration of regrowth following disturbance; e.g. Pugh *et al.*, 2019), agriculture, and 'natural' fluxes, will yield further insights.

V. Conclusions

To evaluate the CO_2-fertilization hypothesis, we synthesized evidence from wide-ranging disciplines within an integrated theoretical framework. We have medium or high confidence that GPP, iWUE, BP, and mortality have all increased over the historical period. However, we frequently have low or medium confidence in the magnitude, and low confidence in how much of the change is attributable to iCO_2.

The complex nature of the problem demands integrated studies, and further integration is required to fully combine the broad evidence in a way that is scale-, bias-, and uncertainty-aware (Box 3). Inference regarding trends and responses (or lack thereof) should always be grounded in the context-dependence and biases associated with a particular study. Further experiments and observations are needed to help reconcile differences among evidence streams. For example, tree-ring sampling at flux sites or

Box 3 Consideration of methods and bias.

In eCO_2 experiments, confinement of roots in pots can limit below-ground resources. While eCO_2 can accelerate leaf area gain in open-grown plants, leading to compound interest that does not occur with closed canopies (Norby *et al*., 1999). These experiments represent early post-disturbance 'reorganizing', and possibly open-canopy ecosystems but are not representative of closed-canopy ecosystems. Oscillating $[CO_2]$ may lessen physiological responses (Allen *et al*., 2020). The step-change in $[CO_2]$ results in a large shift in the ecosystem resource balance (Walker *et al*., 2015), while soil disturbance can increase nutrient availability (Körner, 2006). Many experiments (and evidence themes more broadly) do not quantify total BP, especially root BP. Even the longest-running experiments are short-lived relative to the life span of trees. Landscape-scale atmospheric feedbacks (e.g. increased VPD that could mitigate reductions in transpiration) cannot be accounted for (Leuzinger *et al*., 2015).

Many 'measurements' rely on models in their calculation, and thus have the potential to omit or presuppose a CO_2 effect. For example, satellite gross primary production (GPP; e.g. Sun *et al*., 2018) and net primary production (NPP; e.g. Kolby-Smith *et al*., 2016) are calculated from the fraction of absorbed photosynthetically active radiation (fAPAR) using a light-use efficiency model (Monteith, 1972) that often does not include the CO_2 effect on photosynthesis (De Kauwe *et al*., 2016). Thus, changes in GPP result only from changes in leaf area index (fAPAR) or climate. Conversely, measurement models that include a CO_2 effect are thus not independent of iCO_2 (e.g. iWUE from $\delta^{13}C$, carbonyl sulphide, or isotopomers) and thus have the potential to presuppose a CO_2-related trend.

Carbon isotope discrimination during photosynthesis reduces the $^{13}C : ^{12}C$ ratio ($\delta^{13}C$) in plant material and is used to calculate iWUE from $\delta^{13}C$ (Farquhar *et al*., 1982; Farquhar & Cernusak, 2012). The commonly used model neglects mesophyll and photorespiration discrimination (Farquhar *et al*., 1982; Farquhar & Cernusak, 2012), and accounting for these effects can increase iWUE trends by *c*. 50% (Keeling *et al*., 2017).

Tree-ring trends are subject to sampling and survivorship biases (Brienen *et al*., 2012; Peters *et al*., 2015) that can affect growth trends by up to 200% (Hember *et al*., 2019; Nehrbass-Ahles *et al*., 2014), leading some to question whether tree rings should be used for trend detection at all (Brienen *et al*., 2012). However, tree rings are the only data that offer insights into tree BP since the industrial revolution.

Many studies use tree-ring width as a proxy for wood BP because it is a direct measurement. However, trees grow in three dimensions and change in the one-dimensional ring width does not directly scale with wood volume growth and thus BP in different sized trees. Conversion to the two-dimensional basal area increment (BAI) helps to unify this size mismatch, but again does not account for nonlinear change in wood BP with tree size (Anderson-Teixeira *et al*., 2015). Allometric scaling should be applied to ring width and BAI to attempt a best possible estimate of wood BP (e.g. Dye *et al*., 2016). Static allometric relationships over time can introduce bias where environmental changes have altered resource allocation. For example, shifting allocation from wood to leaves in Russian forests reconciled apparently conflicting inventory data that suggested BP declines, while remote sensing suggested increases (Lapenis *et al*., 2017). Furthermore, wood volume growth does not always scale with BP as wood density can also change (Pretzsch *et al*., 2018).

Forest inventory plots (*c.* 1 ha and less) can undersample mortality, resulting in overestimates of biomass accumulation (Chambers *et al*., 2013). Generally, statistical power for detecting and attributing change in mortality and SOM is often low (Hungate *et al*., 2009; Sulman *et al*., 2018; McMahon *et al*., 2019). Statistical power for detection is low as a result of measurement uncertainty, low signal-to-noise, heterogeneity, and potential pretreatment differences. Low statistical power presents a real challenge for attribution when employing commonly used binary mortality assessments or bulk SOM measurements (Sulman *et al*., 2018; McMahon *et al*., 2019). Furthermore, satellite data, flux towers, and experiments all suffer from short time periods, often with much background variability that can obscure or amplify trends.

Quantification of global 'natural' NBP is confounded with quantification of land-use change-related NBP which is uncertain (95% CI is 92% of the mean flux; Friedlingstein *et al*., 2019). Land-use change-related NBP is calculated using bookkeeping models that account for complex legacy effects and many elements of land-use change, which adds to the uncertainty (Pongratz *et al*., 2014). Furthermore, potentially substantial interactions of land-use change-related NBP and iCO_2 are not considered by these methods. C_{veg} and C_{soil} changes, loss of storage/sink capacity, and potential CO_2 interactions with secondary succession all convolve land-use change and 'natural' NBP fluxes, suggesting a false dichotomy in these flux calculations.

Calculating and interpreting β, or any relative response, is challenging for carbon stocks in which pre-change values can be large, change is the product of two opposing fluxes cumulative over multiple years, and concepts of steady state and nonsteady state apply. Ideally we would like to know β from pre-change steady state to post-change steady state. However, an ecosystem may not be in steady state before change and post-change ecosystems enter a transient phase and can take a long time to reach steady state. Calculated during the transient phase, β will be a function of initial stocks and the developmental stage explored (seedling, sapling, mature tree) and signals will accumulate over time. For ecosystems not in steady state pre-change, β of the changes in the stock increment is not sensitive to initial stocks, but could be large where pre-change increments are small (i.e. when pre-change the system is close to steady state). For steady-state ecosystems pre-change, acknowledgment that β is nonsteady state is needed and a β that explicitly includes temporal scale should be sought.

forest-inventory plots, proximal remote sensing at flux and experiment sites, and model-data integration to reconcile diverse data streams would all help to provide an integrated understanding of this complex problem. A holistic, community-based approach will enable the greatest advances and provide the most robust information to decision-makers.

The required size of climate-change mitigation efforts depends directly on how future terrestrial carbon storage evolves. Evidence for the CO_2-fertilization hypothesis suggests a highly valuable ecosystem service that is buying us time in the fight against climate change, although the size of this subsidy remains unclear. Based on diminishing theoretical GPP responses, probable increasing nutrient limitations, increasing mortality, and other negative temperature-related effects (Peñuelas *et al.*, 2017) it is highly likely that increases in terrestrial carbon storage as a result of iCO_2 will decline into the future. A decline in this subsidy will result in accelerated climate change on the current trajectory of anthropogenic CO_2 emissions.

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Author contributions

APW conceived and wrote the paper, with major contributions from MGDK, AB, KG and SM. APW, ASP and BT collated the data. The ICOFEST meeting was organized by APW, SB, KGC, MGDK, RK, BM, DJPM, RJN and SZ. All authors attended or contributed to the meeting and commented and provided feedback on the manuscript.

ORCID

Anthony P. Walker https://orcid.org/0000-0003-0557-5594
Martin G. De Kauwe https://orcid.org/0000-0002-3399-9098
Ana Bastos https://orcid.org/0000-0002-7368-7806
Soumaya Belmecheri https://orcid.org/0000-0003-1258-2741
Katerina Georgiou https://orcid.org/0000-0002-2819-3292
Ralph F. Keeling https://orcid.org/0000-0002-9749-2253
Sean M. McMahon https://orcid.org/0000-0001-8302-6908
Belinda E. Medlyn https://orcid.org/0000-0001-5728-9827
David J. P. Moore https://orcid.org/0000-0002-6462-3288
Richard J. Norby https://orcid.org/0000-0002-0238-9828
Sönke Zaehle https://orcid.org/0000-0001-5602-7956
Kristina J. Anderson-Teixeira https://orcid.org/0000-0001-8461-9713
Giovanna Battipaglia https://orcid.org/0000-0003-1741-3509
Roel J. W. Brienen https://orcid.org/0000-0002-5397-5755
Maxime Cailleret https://orcid.org/0000-0001-6561-1943
Josep G. Canadell https://orcid.org/0000-0002-8788-3218
Philippe Ciais https://orcid.org/0000-0001-8560-4943
Matthew E. Craig https://orcid.org/0000-0002-8890-7920
David S. Ellsworth https://orcid.org/0000-0002-9699-2272
Graham D. Farquhar https://orcid.org/0000-0002-7065-1971
Simone Fatichi https://orcid.org/0000-0003-1361-6659
Joshua B. Fisher https://orcid.org/0000-0003-4734-9085
Heather Graven https://orcid.org/0000-0003-3934-2502
Lianhong Gu https://orcid.org/0000-0001-5756-8738
Vanessa Haverd https://orcid.org/0000-0003-4359-5895
Kelly Heilman https://orcid.org/0000-0001-5932-1317
Martin Heimann https://orcid.org/0000-0001-6296-5113
Bruce A. Hungate https://orcid.org/0000-0002-7337-1887
Colleen M. Iversen https://orcid.org/0000-0001-8293-3450
Fortunat Joos https://orcid.org/0000-0002-9483-6030
Mingkai Jiang https://orcid.org/0000-0002-9982-9518
Trevor F. Keenan https://orcid.org/0000-0002-3347-0258
Jürgen Knauer https://orcid.org/0000-0002-4947-7067
Christian Körner https://orcid.org/0000-0001-7768-7638
Sebastian Leuzinger https://orcid.org/0000-0001-9306-5281
Yao Liu https://orcid.org/0000-0003-2783-3291
Natasha MacBean https://orcid.org/0000-0001-6797-4836
Yadvinder Malhi https://orcid.org/0000-0002-3503-4783
Tim R. McVicar https://orcid.org/0000-0002-0877-8285
Josep Penuelas https://orcid.org/0000-0002-7215-0150
Julia Pongratz https://orcid.org/0000-0003-0372-3960
A. Shafer Powell https://orcid.org/0000-0002-9622-0061
Manon E. B. Sabot https://orcid.org/0000-0002-9440-4553
Juergen Schleucher https://orcid.org/0000-0002-4815-3466
Stephen Sitch https://orcid.org/0000-0003-1821-8561
William K. Smith https://orcid.org/0000-0002-5785-6489
Benjamin Sulman https://orcid.org/0000-0002-3265-6691
Benton Taylor https://orcid.org/0000-0002-9834-9192
César Terrer https://orcid.org/0000-0002-5479-3486
Margaret S. Torn https://orcid.org/0000-0002-8174-0099

Kathleen K. Treseder https://orcid.org/0000-0003-2847-6935
Anna T. Trugman https://orcid.org/0000-0002-7903-9711
Susan E. Trumbore https://orcid.org/0000-0003-3885-6202
Phillip J. vanMantgem https://orcid.org/0000-0002-3068-9422
Steve L. Voelker https://orcid.org/0000-0002-0110-3381
Mary E. Whelan https://orcid.org/0000-0002-2067-1835
Pieter A. Zuidema https://orcid.org/0000-0001-8100-1168

Data availability

Data and analysis scripts used in this publication can be found at ESS-DIVE (https://data.ess-dive.lbl.gov/view/doi:10.15485/1644687).

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Supporting Information

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

Fig. S1 Comparison of alternatives methods to calculate β.

Fig. S2 Evidence β values for GPP, WUE, and BP.

Fig. S3 Evidence β values for k_{veg}, k_{soil}, NEP, and $C_{veg,increment}$.

Fig. S4 Evidence β values for C_{veg}, C_{soil}, and C_{eco}.

Notes S1 Standardizing CO_2 responses with a β factor.

Notes S2 Calculation of β from different data types.

Notes S3 Modelling leaf and canopy physiology.

Table S1 Theoretical β values for photosynthesis.

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