Commentary

The effects of rising CO_2 concentrations on terrestrial systems: scaling it up

Since the Industrial Revolution, atmospheric CO_2 concentrations have increased by *c.* 50%, from 280 ppm to a current level of 415 ppm and rising (Ciais *et al.*, 2013). But CO_2 concentrations would be even higher if the terrestrial biosphere was not acting as a carbon sink, absorbing *c.* 30% of the CO_2 we emit every year (Le Quéré *et al.*, 2016). Understanding how increasing CO_2 concentrations will alter the ability of vegetation and soils to sequester carbon is therefore critical for predicting the trajectory of future climate change, since a reduction in this carbon sink would cause a more rapid accumulation of CO_2 in the atmosphere (Dusenge *et al.*, 2019). In this issue of *New Phytologist*, Walker *et al.* (2021; pp. 2413–2445) synthesize data from an incredibly broad range of sources, including herbaria, free air CO_2 enrichment (FACE) studies, ice cores, eddy covariance sites, and remote sensing, and examine an enormous diversity of measurements (such as soil respiration rates, glucose isotopomers from leaves, tree ring width data, stream-gauges for runoff, and direct atmospheric CO_2 measurements) to address the question of how increasing CO_2 concentrations are affecting the carbon uptake capacity of our planet.

> *'. . . changes in plant carbon, nitrogen and water dynamics due to rising CO_2 concentrations cascade throughout ecosystems, with global impacts that are much less well understood.'*

The type of data synthesis Walker *et al.* undertake is rare but exceedingly valuable, since it collates biological responses to elevated CO_2 that may not be familiar to researchers who focus on a particular scale or domain. To enable direct comparison between such disparate data streams, Walker *et al.* express the results of the collected studies as relativized β-factors, which provide an estimate of the change in the measured variable per unit change in CO_2 concentration (i.e. a β-factor of 1 means that the variable rises in direct proportion to the increase in CO_2 concentration). To help the reader weigh the degree of agreement among studies of a given variable, Walker *et al.* also assigned a simple confidence metric to aid interpretation. The authors find that there is strong evidence and high confidence that carbon uptake, water use efficiency, and biomass production have increased concurrently with rising CO_2 concentration, consistent with theoretical expectations. However, they also report a lower confidence in our ability to quantify the magnitude of these changes, or to attribute these shifts to rising CO_2 concentrations. Furthermore, the theoretical magnitude of many responses is not consistent with observations, highlighting the need for improved process knowledge of ecosystem feedbacks.

A change in atmospheric CO_2 cascades through biological systems to affect many processes. The immediate effects of exposing vegetation to elevated CO_2 are an increase in photosynthesis, a decrease in stomatal conductance and an increased growth rate (Dusenge *et al.*, 2019). Over longer timescales, these changes in leaf carbon and water fluxes can induce acclimation, whereby plants reduce their investment of leaf nitrogen in the carbon-fixing enzyme Rubisco, alter their stomatal traits, and adjust their canopy structure, hydraulic architecture and biomass allocation patterns (Ainsworth & Long, 2005; De Graff *et al.*, 2006). These short- and longer-term effects of elevated CO_2 levels on plant physiology and productivity are well known and relatively well understood.

However, these changes in plant carbon, nitrogen and water dynamics due to rising CO_2 concentrations cascade throughout ecosystems, with global impacts that are much less well understood. If reductions in leaf-level stomatal conductance decrease whole plant canopy transpiration, this could reduce plant water stress (Leakey *et al.*, 2009) and lead to increased run-off at continental scales (Betts *et al.*, 2007). Yet an increase in leaf area index (i.e. canopy density) under high CO_2 could offset leaf-level water savings at the whole plant level (Way *et al.*, 2010; Gray *et al.*, 2016), thereby increasing drought stress and minimizing changes in water cycling at the ecosystem level. Similarly, increased soil water availability due to lower whole-plant transpiration rates in high CO_2 can alter competition and increase the abundance of less drought-adapted species (Fay *et al.*, 2012), which could eventually negate the original change in soil water content at the community level. One can consider similar types of feedbacks on litter decomposition. Increased litter production and allocation of carbon to belowground tissues and processes is common under elevated CO_2 concentrations (De Graaf *et al.*, 2006), and these effects can stimulate microbial biomass and soil respiration rates, which can, in turn, increase soil organic matter (SOM) decomposition rates (Drake *et al.*, 2011; van Groenigen *et al.*, 2014). However, the higher carbon : nitrogen ratios of leaves produced in a high CO_2 environment can reduce the decomposability of litter generated by elevated CO_2-grown plants (Cotrufo *et al.*, 1994), which may instead suppress SOM decomposition rates. Thus, the

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net effect of rising CO_2 at the ecosystem level on SOM decomposition may vary considerably, depending on the relative strengths of these various effects.

Since the potential for these types of feedbacks increases as we consider systems with greater biological complexity, we may expect that as we scale up from a leaf to a whole plant to an ecosystem and, finally, to the globe, the effects of elevated CO_2 should become weaker and more variable (Fig. 1). Walker *et al.* report on how a number of different variables are affected by rising CO_2 concentrations, including variables related to plant carbon gain, water use efficiency and biomass production, and for some of these variables, they provide data across a broad range of biological scales. We therefore examined whether the β-factors in Walker *et al.* for plant carbon uptake (i.e. either leaf-level light-saturated net photosynthetic rates (A_{sat}) or ecosystem and global estimates of gross primary productivity (GPP)) and instantaneous water use efficiency (iWUE) varied in a predictable manner across biological scales as proposed in Fig. 1. To do this, we grouped the A_{sat} and GPP data in Table 2 of Walker *et al.* into either leaf, ecosystem or global scale estimates of vegetation carbon gain (as there were no whole plant-level data) and similarly grouped the iWUE data into leaf, tree, ecosystem or global data categories. While we appreciate that there are significant limitations to our analysis – e.g. small sample sizes, some studies are over-represented, and many other limitations, many of which are detailed by Walker *et al.* themselves – there are few data sets of this nature available, and the standardized β-factors allow one to compare data across scales in a way that the original publications do not.

With those (substantial) caveats in mind, let's look at the data. For carbon gain, we found no decrease in β-factor with increasing biological scale (Fig. 2). While there was considerably more variation in estimates of global responses of GPP to rising CO_2 than there was in the leaf and ecosystem-level GPP data (Fig. 2), this is correlated with the greater sample size in the global-scale data and is likely artifactual. By contrast, there was some indication that the impact of rising CO_2 concentration on iWUE may decline as the biological scale considered increases (Fig. 2), though there are far too few data at the ecosystem and global scales to make broad

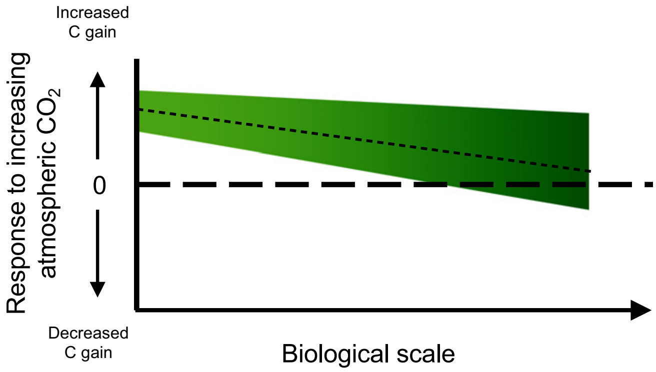

Fig. 1 Conceptual figure of how the effects of elevated atmospheric CO_2 concentrations on terrestrial systems (such as carbon gain) may vary across differing biological scales. At the leaf scale, elevated CO_2 effects are often measured on healthy sun leaves from well watered and fertilized C_3 plants and, despite acclimation, high CO_2 usually stimulates leaf-level carbon gain. But there may be less stimulation of whole-plant carbon gain in response to rising CO_2, as well as more variation between individual plants, since shade leaves will be less responsive to increased CO_2 than sun leaves, and changes in hydraulic traits and biomass allocation can also impact canopy-level carbon gain. At the community and ecosystem levels, gross primary productivity (GPP) may be less positively affected by rising CO_2 concentrations than in individual plants because of the increasing likeliness of a range of feedbacks related to plant–plant competition, plant–soil feedbacks and variation in CO_2-sensitivity between plant functional types (such as C_4 species). These feedbacks become even more likely when considering the global scale estimates of CO_2 sensitivity, as some ecosystems (like nutrient-limited regions (Ellsworth *et al*., 2017) and cold regions with lower photorespiratory costs (Hickler *et al*., 2008)) may show very low CO_2 sensitivity, implying that global GPP would likely be less sensitive to rising CO_2 than studies from commonly-studied individual ecosystems. Similar scaling effects are likely for other variables as the biological complexity of the system assessed increases. The thin dashed line represents the mean response of the variable to rising CO_2 concentrations; the green shading represents increasing biological scale and complexity.

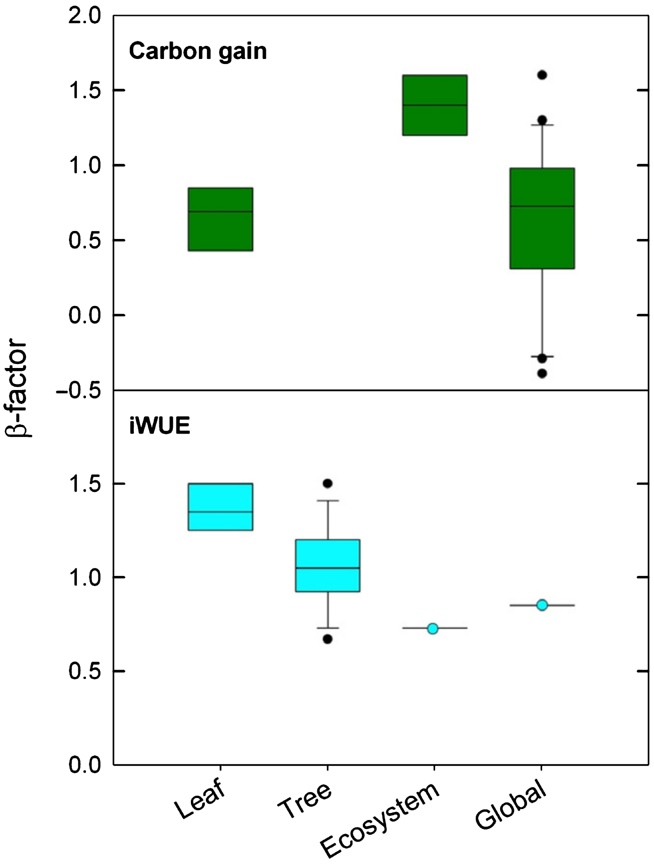

Fig. 2 Variation in β-factors for the impact of rising atmospheric CO_2 concentrations on carbon gain (light-saturated net CO_2 assimilation rates for leaves or gross primary productivity for trees, ecosystems and global scales) and instantaneous water use efficiency (iWUE for all four scales) in terrestrial systems across different biological scales. The β-factor provides an estimate of the change in the measured variable per unit change in CO_2 concentration. Leaf, leaf-level data; Tree, tree-level data; Ecosystem, ecosystem-level data; Global, global data. Data from Table 2 in this issue of *New Phytologist* by Walker *et al*. (2021; pp. 2413–2445). Boundaries of the boxes indicate the 25th and 75th percentiles, the horizontal line in the box indicates the median, whiskers indicate the 10th and 90th percentiles and black circles show outliers. Where there is only a single data point, the point is shown with a colored circle and a horizontal line

conclusions. Overall, what the analysis really emphasizes is the need for more data on how elevated CO_2 alters plant carbon, nutrient and water cycling across multiple scales. We therefore fully support the recommendation from Walker *et al.* that researchers should quantify the effect of high CO_2 concentrations at multiple scales within their own study site whenever possible, such as by measuring leaf-level gas exchange and sampling tree rings at eddy covariance sites, to better allow us to improve our understanding and model representation of processes at leaf-, whole plant-, ecosystem- and global-scales.

The Walker *et al.* review provides us with the clearest view yet of how rising CO_2 concentrations are affecting carbon cycling on Earth. That one of the main conclusions of such a herculean effort is that we have relatively little confidence in attributing recent increases in GPP, iWUE and biomass production to increasing CO_2 concentrations should be taken as a call to arms by the global change biology community to invest in multi-disciplinary research that aims to improve mechanistic understanding.

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