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Re-analysis of plant CO_2 responses during the exponential growth phase: interactions with light, temperature, nutrients and water availability

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Abstract. Many short-term experiments have been conducted under increasing CO_2 but results have been varied and have not yet led to a conclusive quantitative understanding of the CO_2 response of plant growth. This may have been partly due to a lack of explicit consideration of the positive feedback inherent in plant growth during periods of exponential growth. This feedback can increase an initial physiological enhancement of relative growth rate (RGR) into a much larger biomass enhancement. To overcome this problem, we re-analysed existing experimental data from 78 publications. We calculated the RGRs of C_3 plants and their relative enhancement under elevated CO_2 and derived response indices that were independent of the duration of experiments and the RGR at normal atmospheric CO_2. The RGR of unstressed plants increased by $14 \pm 2\%$ under doubled CO_2, with observed RGR enhancement linearly correlated with calculated photosynthetic enhancements (based on the Farquhar-von Caemmerer-Berry photosynthesis model), but at only half their numeric values. Calculated RGR enhancements did not change significantly for temperatures from 12 to 40°C, but were reduced under nutrient limitation, and were increased under water stress or low irradiance. We concluded that short-term experiments can offer simple and cost-effective insights into plant CO_2 responses, provided they are analysed by calculating relative changes in RGR during the strictly exponential initial growth phase.

Additional keywords: nutrient limitation, photosynthesis, PAR, photosynthetically active radiation, relative growth rate, RGR, water limitation.

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Introduction

The pre-industrial atmospheric carbon dioxide concentration [CO_2] was ~280 µmol mol^{-1}. It is currently increasing by ~2 µmol mol^{-1} year^{-1} and reached nearly 400 µmol mol^{-1} by 2013 (Hartmann *et al*. 2013). Plants grow by absorbing CO_2 from the atmosphere, and current atmospheric concentrations are less than saturating for photosynthesis for most plants (e.g. Farquhar and von Caemmerer 1982). Plant growth is therefore likely to increase with increasing atmospheric [CO_2] (Franks *et al*. 2013). The important question is by how much?

For modelling studies of plant productivity under climate change (e.g. Medlyn *et al*. 2011; Kirschbaum *et al*. 2012; Peters *et al*. 2013; Reyer 2015), it is possible to compare growth responses to changing temperatures or rainfall with observed growth in regions that currently experience different climatic patterns. This is more difficult for responses to [CO_2] as available observations are largely restricted to a limited number of studies with experimentally altered CO_2 concentrations (Hickler *et al*. 2015). Therefore, CO_2 responses remain one of the most uncertain aspects of predicting future plant performance.

One can readily observe short-term photosynthetic responses to [CO_2], and studies with C_3 plants have demonstrated consistent and positive photosynthetic responses to increasing [CO_2] (Drake *et al*. 1997; Long *et al*. 2006; Kirschbaum 2011). These responses are generally in line with our understanding of the fundamental biochemical processes that govern leaves' responses to their external environment (Farquhar and von Caemmerer 1982; Franks *et al*. 2013). However, photosynthetic carbon gain interacts with other plant processes. The ultimate growth response to elevated [CO_2], therefore, cannot simply be equated with the CO_2 response of photosynthesis (e.g. Poorter *et al*. 2013).

To better understand the response of plant growth, many experiments have been conducted over relatively short time frames under growth-chamber or glasshouse conditions, using plants grown in pots or hydroponically (e.g. Kimball 1983; Poorter 1993; Pinkard *et al*. 2010). Other experiments have been conducted in the field using open-top chambers or free air CO_2 enrichment (FACE) methods (Ainsworth and Long 2005; Norby and Zak 2011). The latter is generally considered to create the most realistic conditions as there are no artificial below- and aboveground barriers to modify the plants' environment.

However, FACE experiments tend to be very resource intensive and costly (Pinkard *et al*. 2010), which allows only limited exploration of the response of different species or

$[CO_2]$ × environment interactions. Responses also vary from year-to-year simply because of uncontrolled climatic variability between years (e.g. Annicchiarico 2002) or inevitably-fluctuating CO_2 concentration in FACE studies (Bunce 2013). This makes it difficult to investigate CO_2 responses systematically under a variety of co-limitations, or for a range of different plant species. Short-term experiments under controlled conditions therefore retain an important role in advancing the understanding of the interaction between plant responses to elevated $[CO_2]$ and other environmental factors.

Interpreting experimental findings

In its simplest from, short-duration experiments can be analysed by comparing the biomass of plants grown at elevated $[CO_2]$ for a given length of time with that of plants grown at control $[CO_2]$. This ratio is termed the biomass enhancement ratio (BER). Poorter and Navas (2003) compiled results from a wide range of experiments and found that BERs averaged ~1.45 for herbaceous and 1.48 for woody plants (Table 1).

A different way to analyse CO_2 responses of young plants is by calculating their relative growth rate (RGR). Plants typically grow exponentially for some time before growth falls below that predicted by on-going exponential growth. Plant growth during and after the exponential growth phase can be described by a simple growth model (Fig. 1; Kirschbaum 2011). This allows the analysis of the interaction between time, the RGR of plants grown under low $[CO_2]$ (RGR_{350}) and the 'relative' enhancement of RGR by elevated $[CO_2]$ (RERC). The model by Kirschbaum (2011) assumes a constant ratio of plant size to leaf area index, a RERC of 10% (Poorter and Navas 2003), and an eventual cessation of exponential growth through increasing self-shading as is typically observed in longer-term experiments (e.g. Poorter *et al*. 1988; Körner 2006).

Loehle (1995), Gifford *et al*. (1996), and Kirschbaum (2011), using models like the one described above, showed that the BER during the exponential growth phase can substantially exceed the enhancement calculated on the basis of the underlying RERC. BERs depend not only on a plant's inherent responsiveness to elevated $[CO_2]$, but also on time (Fig. 1*c*) and on RGR_{350} (Fig. 2). Over the initial growth phase, after imposition of CO_2 treatments, BERs increase with time because the positive feedback during exponential growth can amplify the initial CO_2 response (Fig. 1*c*; Loehle 1995; Gifford *et al.* 1996; Körner 2006; Kirschbaum 2011). Put simply, on the first day of a CO_2 treatment, one can compare the CO_2 response of two plants of the same size and with the same leaf area. On day 2, however, the high-CO_2 plant will benefit not only from higher CO_2, but also from its slightly higher leaf area developed during the previous day's high-CO_2 exposure. This amplification is small at first, but increases over time to become quantitatively important (Fig. 1*c*).

However, RGRs cannot remain at peak values for very long, but begin to decrease when other growth limitations such as pot volumes or physical space that leads to self-shading, provide additional over-riding growth constraints (Gifford *et al.* 1996; Fig. 1*b*). If these effects are directly linked to plant size, they will have a greater effect on high- than low-$[CO_2]$ grown plants (Fig. 1*b*) so that BERs decrease when these constraints take effect (Fig. 1*c*). The model also shows that for a given length of experiments, BERs correlate with RGR_{350} (Fig. 2). This is because with increasing RGR_{350}, the positive feedback during exponential growth can more rapidly amplify the initial RERC signal into the numerically much greater BER.

Table 1. Biomass enhancement ratios (BERs) in response to elevated $[CO_2]$ for different plant groups, or for plants subject to different co-limitations

The data shows total dry mass stimulation for vegetative plants harvested at the end of the experimental periods. Data were summarised from a range of prior studies by Poorter and Navas (2003)

Plant group/co-limitation	BER
Woody plants	1.48
All herbaceous plants	1.45
Fast-growing herbaceous plants	1.59
Slow-growing herbaceous plants	1.25
Low-temperature grown plants	1.27
Low-PAR grown plants	1.52
Low-nutrient grown plants	1.25
Water-stressed plants	1.51

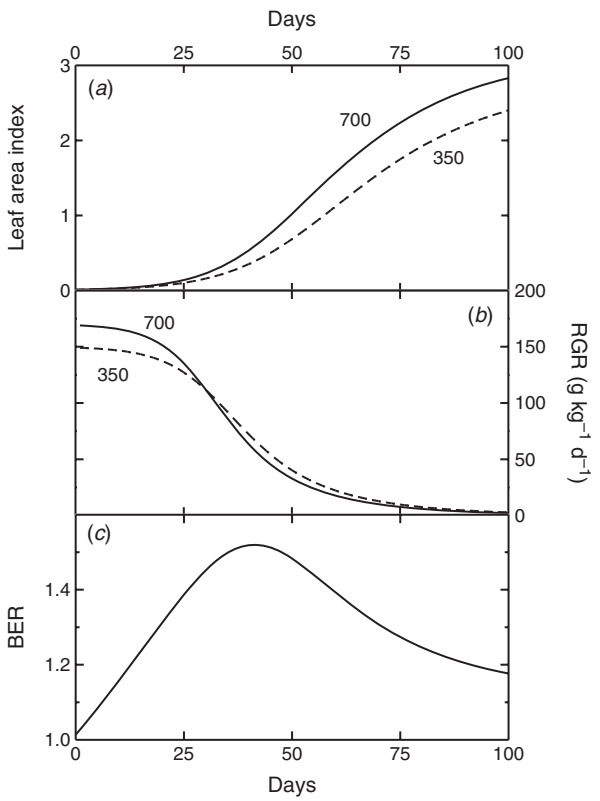

Fig. 1. Leaf area development over time in high (solid lines; 700 µmol mol^{-1}) and low $[CO_2]$ (dashed lines; 350 µmol mol^{-1}) based on the simple model by Kirschbaum (2011), showing leaf area index (*a*), the relative growth rate (*b*) and biomass enhancement ratio (*c*) under elevated and normal $[CO_2]$ as a function of time (assuming a constant ratio of leaf area to total biomass). Simulations assume an RGR_{350} of 150 g kg^{-1} day^{-1} and RERC of 10%, the average values reported by Poorter and Navas (2003) for experimental observations.

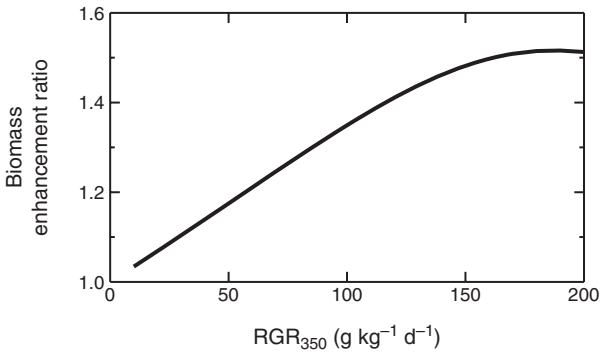

Fig. 2. Biomass enhancement ratios as a function of the relative growth rate at ambient [CO_2]. Model assumptions are the same as used for Fig. 1. The results shown here are for 34 days of simulations (the median length of CO_2 experiments with herbaceous plants).

Experimental observations summarised by Poorter and Navas (2003) indicated that BERs varied with changes in plant type or growing conditions, and faster-growing species had greater BERs than more-slowly growing plants (Table 1). This could mean that faster-growing species are inherently more responsive to elevated [CO_2] than slower-growing species. In contrast, Poorter and Navas (2003) also showed that the 'absolute' enhancement of RGR increased linearly with plants' RGR_{350}. This meant that the 'relative' enhancement of relative growth rate by elevated [CO_2] (RERC) remained constant and was therefore independent of the RGR. If fast- and slow-growing plants had the same RERC, it implies that there are no fundamental physiological differences in their responses to elevated [CO_2]. Patterns emerging from the analyses of BERs can thus lead to different conclusions from those derived from analyses of RERCs.

Table 1 also shows that BERs of water-stressed plants and plants grown under low photosynthetically active radiation (PAR) were the same as those of plants grown without limitations (Poorter and Navas 2003). This conflicts with the theoretical understanding of the photosynthetic CO_2 response of plants that predicts greater CO_2 responsiveness for water-limited than non-limited plants (e.g. McMurtrie *et al*. 2008). When plants are grown with non-limiting water supply, any CO_2 response must be based on the enhancement of photosynthesis by increasing CO_2. Under water limitation, however, increasing [CO_2] also leads to partial stomatal closure (e.g. Morison 1985; Franks *et al*. 2013), which enhances plant water-use efficiency. As water-use efficiency is increased by increases in photosynthesis and decreases in stomatal conductance, it is numerically greater than the photosynthetic enhancement alone. This leads to the expectation of relatively greater CO_2 responses under water-limited than well-watered conditions (e.g. McMurtrie *et al*. 2008). However, the BER data in Table 1 imply that water-limited and well-watered plants had the same CO_2 responsiveness.

For plants grown under PAR-limited conditions, RERC might also be higher because plants operate closer to their light-compensation point where the ratio of photosynthesis to respiration is closer to one (e.g. Sims and Pearcy 1994). Any enhancement of photosynthesis could thus lead to greater relative growth enhancements under low PAR than for plants grown under high PAR where the photosynthesis to respiration ratio is already higher. Under PAR-limited conditions, plants are also more likely to be limited by carbohydrate availability than under high PAR. When plants have excess carbohydrate resources, photosynthesis may be downregulated which could reduce any beneficial effect of elevated [CO_2]. This is more likely to occur in high-PAR grown plants than in those grown under low PAR, leading to the expectation of greater CO_2 responses in low-PAR grown plants. However, this theoretical expectation also conflicts with the observation of similar BERs for plants grown under low and high PAR (Table 1).

However, explicit consideration of the positive feedback during exponential growth could reconcile these apparently conflicting findings. Plants growing under water-stressed or low-PAR conditions must have had lower RGR_{350} than non-stressed plants. If their RERCs had been the same as those of non-stressed plants, it should have led to lower BERs (cf. Fig. 2). Instead, their BERs remained similar to that of unstressed plants (Table 1), which could only be possible if the RERC of water- and PAR-limited plants had actually been greater than that of unstressed plants. At a direct physiological level, stressed plants could thus have responded more strongly to elevated [CO_2] (as expressed in higher RERC) than unstressed plants, but because of the stressed plants' lower RGR_{350} that would not have led to enhanced BERs.

Nutrient-limited plants must have also had lower RGR_{350} than plants grown with adequate nutrition. Their observed lower BERs (Table 1), therefore, could have also been due to their lower RGR_{350} rather than indicate a lower inherent CO_2 responsiveness of nutrient-limited plants. Put differently, even if RERC had remained unaffected by nutrient limitations, the BERs of nutrient-limited plants could have still been reduced through their lowered RGR_{350}, leaving it uncertain whether CO_2 responsiveness interacts with nutrient limitations.

Photosynthetic theory also clearly shows a strong [CO_2] × temperature interaction, with much greater CO_2 responsiveness at higher temperatures (e.g. Farquhar and von Caemmerer 1982; Medlyn *et al*. 2002). This has led to the expectation of similar interactions between temperature and plant-growth responses to elevated [CO_2] (e.g. Long 1991; Kirschbaum 1994). A critical analysis of experimental observations is needed to ascertain whether that expectation based on photosynthetic observations is consistently expressed in plant growth responses.

In the present work, we have re-analysed available reports of CO_2 responses during plants' exponential growth phase in combination with temperature, and PAR, nutrient or water limitations. We analysed each reported response pattern with respect to calculated RGR_{350} and the relative enhancement of respective RGRs under elevated CO_2 (RERC). Through these analyses, we tried to obtain insights into the physiological relationships between the CO_2 responses of plants and these different co-limiting factors. This included only C_3 plants as the photosynthetic CO_2 response is very different for C_3 and C_4 plants (e.g. Ainsworth and Long 2005) and therefore likely to interact differently with other growth-limiting factors.

Materials and methods

We obtained data from 78 experiments published in the literature. From each experiment, we extracted information on experimental

conditions, such as mean daytime temperatures, high and low [CO_2], and the imposition of any PAR, nutrient or water limitations. We used observations of total plant dry weights, or the nearest equivalents (such as aboveground biomass when total biomass was not given), reading values from available graphs or tables and fitting a simple growth model to each dataset to derive RERCs under the experimental conditions. The principal criterion for inclusion in this analysis was for growth to be exponential for at least the early part of respective experimental periods so that relative growth rates could be calculated. All data presented below were derived from these experimental data obtained from the literature. Details of the data sources have been given in the Supplementary Material, which is available online.

In the model, the growth increment of biomass dB/dt was calculated at daily intervals as:

$$\mathrm{d}B/\mathrm{d}t = Be^{k_1}e^{-k_2B}, \tag{1}$$

where B is biomass, t is time, and k_1 and k_2 are parameters fitted to respective datasets. In this expression, the first exponential term described the exponential growth phase and the second exponential term the down-turn in growth towards the end of the exponential growth phase.

The inclusion of this second exponential term allowed the incorporation of data obtained beyond the initial exponential growth phase, although data that deviated too strongly from exponential growth were excluded from the analysis. The asymptotic term k_2 was constrained to be the same for plants exposed to different [CO_2], but was allowed to differ between plants exposed to different co-limiting factors. This implicitly assumed that growth after the exponential phase was reduced through factors that could be linked to plant biomass *per se* with no difference between high- and low-[CO_2] grown plants. It meant that such size limitations affected high-[CO_2] grown plants slightly earlier than low-[CO_2] grown plants (cf. Poorter *et al*. 1988).

Initial biomass at time 0 was set to the same value for plants grown under different conditions and different [CO_2]. This was generally a fitted value based on observations reported for older seedlings unless the actual biomass of plants at the start of respective treatments was reported. Goodness of fit was assessed by residual sums of squares of log-transformed biomass data. For each data pair at high and low [CO_2], we thus obtained two k_1 values, $k_{1,\mathrm{low}}$ and $k_{1,\mathrm{high}}$, which represented the fitted values at low and high [CO_2]. The observed relative CO_2 enhancement of RGR, c_{enh}, is the physiological relevant measure of the growth enhancement under specific experimental conditions. It was calculated as:

$$c_{\mathrm{enh}} = \frac{(k_{1,\mathrm{high}} - k_{1,\mathrm{low}})}{k_{1,\mathrm{low}}}. \tag{2}$$

Many experiments used 350 for low, and 700 μmol mol^{-1} for high [CO_2], but other experiments used a variety of concentrations. To improve comparability of the findings from different studies, all data were normalised by calculating the relative enhancement of relative growth rate by [CO_2], RERC, at standardised high and low [CO_2] of 350 and 700 μmol mol^{-1} based on the theoretical CO_2 response of C_3 plants:

$$\mathrm{RERC} = c_{\mathrm{enh}}\frac{E_{350,700}}{E_{\mathrm{low,high}}}, \tag{3}$$

where $E_{350,\ 700}$ is the theoretical enhancement of photosynthesis calculated under 350 and 700 μmol mol^{-1}, respectively, and $E_{\mathrm{low,high}}$ is the calculated enhancement under the actual low and high [CO_2] used in respective experiments.

The CO_2 enhancement of photosynthesis, $E_{\mathrm{low,high}}$, was calculated as:

$$E_{\mathrm{low,high}} = \left(\frac{C_{\mathrm{high}}}{C_{\mathrm{low}}} - 1\right), \tag{4}$$

where c_{high} and c_{low} are photosynthetic responses at high and low [CO_2] respectively.

The theoretical photosynthetic CO_2 response, c_{p}, for RuBP-regeneration limited photosynthesis was calculated following Kirschbaum (1994) as:

$$c_{\mathrm{p}} = \frac{c_{\mathrm{i}} - \Gamma_*}{c_{\mathrm{i}} + 2\Gamma_*}, \tag{5}$$

where c_{i}, is the intercellular [CO_2] and Γ_* is the CO_2 compensation point in the absence of non-photorespiratory respiration.

The c_{i} was taken to be two-thirds of ambient [CO_2] and assumed to remain constant under changing [CO_2] (Ball *et al*. 1987). Γ_* was calculated following Bernacchi *et al*. (2001), as:

$$\Gamma_* = 42.75e^{\left(15.26\frac{T-25}{T+273.15}\right)}, \tag{6}$$

where T is the estimated mean daytime temperature.

Differences in CO_2 stimulation under different co-limitations (low PAR, nutrient or water stress), ΔRERC, were simply calculated as:

$$\Delta\mathrm{RERC} = \mathrm{RERC_s} - \mathrm{RERC_o}, \tag{7}$$

where $\mathrm{RERC_s}$ and $\mathrm{RERC_o}$ are the respective CO_2 stimulations under stressed and optimal conditions.

The extent of growth-limitation by the co-limitations, g_{lim}, was calculated as:

$$g_{\mathrm{lim}} = \frac{k_{1,\mathrm{low(s)}}}{k_{1,\mathrm{low(o)}}}, \tag{8}$$

where $k_{1,\mathrm{low(s)}}$ and $k_{1,\mathrm{low(o)}}$ are the calculated $\mathrm{RGR_{350}}$ for stressed and optimal growth conditions, respectively. The closer this ratio is to 0, the stronger is the environmental limitation, while the ratio becomes 1 for optimal growth.

Initial parameter fitting was done using a customised Excel spreadsheet, using Excel's 'Solver' add-in to find parameter sets with minimised residual sums of squares. A copy of the spreadsheet is available from the authors upon request. Subsequent statistical analyses were undertaken using GENSTAT 12 (VSN International, Hemel Hempstead, UK). Regression analysis was used to assess correlations between RERC and photosynthetic CO_2 enhancement, and between Δ*RERC* and various co-limiting factors. Two-sample, two-tailed, *t*-tests were used to assess for differences between woody and herbaceous plants. Differences were considered to be significant if $P < 0.05$.

Illustrating the parameterisation routine

Use of the fitting and analysis routine is demonstrated in Fig. 3 with a dataset (for well-watered plants) obtained from Townend (1995). Over the initial growth phase to about day 70, data followed an exponential growth pattern, shown by the near-linear relationships on the logarithmic plots in Fig. 3*c*, *d*.

Growth then increasingly fell below exponential growth after day 70, with data points after this time falling below an implicit straight line fitted to the early points that indicated exponential growth. The second exponential term in Eqn 1 allowed the reduced growth to be described adequately as well. Townend (1995) also reported some data beyond day 180, but observations at those later stages deviated so strongly from exponential growth that those data were excluded from the analysis.

The key derived parameters for the present work were the initial slopes of the fitted curves over the exponential growth phase (equivalent to k_1). However, it was often difficult to confidently describe parameters for the exponential phase alone because most experiments provided few data points over that period, and the duration of the exponential growth period was also often uncertain. These problems were lessened by use of Eqn 1 that allowed data from the early post-exponential phase to be included as well.

The initial slopes of the curves fitted to these data gave the RGRs under different conditions. The relative difference between RGRs at high and low $[CO_2]$ (ΔRERC) was taken as the appropriate measure of the plants' CO_2 response as it was independent of the duration of experiments and thus unconfounded by time or other factors. This CO_2 response could then be related to interactions with other co-limiting factors. In this particular example (Fig. 3), increasing $[CO_2]$ increased RGR by 19% (RERC = 0.19) for plants with adequate nutrition, and by 11% for nutrient-limited plants.

Results

Growth enhancements at different $[CO_2]$

Different experiments used different combinations of low and high $[CO_2]$, with only ~12% of experiments using the 'standard' combination of 350 and 700 µmol mol^{-1}. This provided an opportunity to assess the response of the relative growth enhancements of RGR, c_{enh}, to differences in the combination of low and high $[CO_2]$. RERC differs from c_{enh} through its normalisation to a standard combination of low and high $[CO_2]$.

Photosynthetic enhancements were calculated from mean daytime temperature and the experimental low and high $[CO_2]$ but used no actual measurements from those experiments whereas c_{enh} was calculated from observed growth measurements. Although individual c_{enh} observations showed considerable scatter, mean c_{enh}, calculated over defined ranges of photosynthetic enhancement, were tightly and linearly correlated ($r^2 = 0.94$, $P < 0.001$) with photosynthetic enhancements (Fig. 4). We also compared the response of woody and herbaceous plants, but found no significant difference in the deviation of individual data from the line of best fit between woody and herbaceous plants ($P = 0.070$).

This linear correlation between c_{enh} and calculated photosynthetic enhancement (in the averaged data) was surprisingly tight across a wide range of calculated photosynthetic CO_2 enhancements, with no indication for c_{enh} to have deviated from a linear relationship over the whole range of experimental conditions. However, the observed c_{enh}

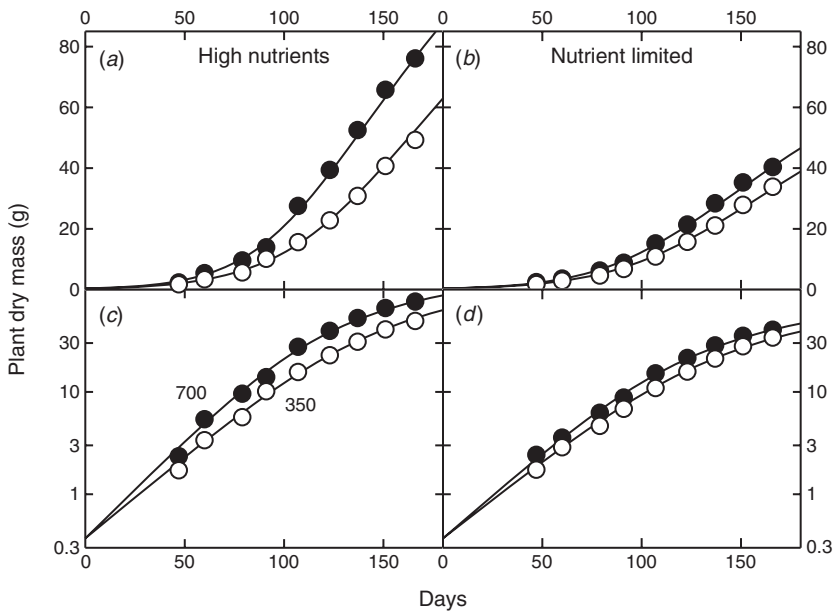

Fig. 3. Illustration of the data analysis method used here, demonstrated with fertilised (*a*, *c*) and nutrient-limited data (*b*, *d*) from Townend (1995). Symbols show the observations and solid lines the fitted model (Eqn 1). Open symbols refer to plants grown at 350 and closed symbols to plants grown at 700 µmol mol^{-1}. Data in (*c*, *d*) are shown on a logarithmic scale. The lines were calculated with $k_{1,high(o)} = 0.044$ day^{-1}, $k_{1,low(o)} = 0.037$ day^{-1}, $k_{1,high(s)} = 0.039$ day^{-1}, and $k_{1,low(s)} = 0.035$ day^{-1}, leading to $RERC_o = 0.19$, $RERC_s = 0.11$ and $g_{lim} = 0.95$.

was only about half (0.495) of the calculated photosynthetic enhancement (Fig. 4), indicating that some other plant factors (i.e. changes in specific leaf area) or negative feedback factors (e.g. in response to excess carbohydrate) caused the ultimate growth response to be only half of the initial photosynthetic enhancement.

We then investigated the interactions between CO_2 enhancement and other physiological variables after normalising observed CO_2 enhancements to a standard combination of low and high [CO_2], designated as RERC.

Interactions with temperature

Fig. 5*a* shows RERCs observed at different temperatures in individual studies. There was no indication of any systematic differences between woody and herbaceous plants ($P = 0.058$). Fig. 5*b* analyses these data further by calculating means and confidence intervals over 5°C temperature intervals. The overall mean RERC was 0.14 ± 0.02, with no significant change over temperatures from 12 to 40°C. It is readily apparent that the observed data did not conform to the theoretical relationship, with observations exceeding the expected CO_2 enhancement at cold temperatures and falling below it at higher temperatures.

Observed RGR_{350} had an optimum between 25 and 30°C (Fig. 5*c*), but the below-optimum reductions in RGR_{350} were not extreme at either high or low temperatures. The observations thus covered a range of physiologically meaningful conditions. It discounted the possibility of high-temperature grown plants having failed to display the expected CO_2 responsiveness because of growth under biologically damaging conditions. This was further confirmed by plotting RERC against RGR_{350} (Fig. 6). RERC was independent of RGR_{350}, with no statistically significant correlation between them. The key observation here is that there was no positive correlation between RGR_{350} and RERC. Had plants with low RGR_{350} also shown low RERCs, it might have indicated that plants experiencing physiologically extreme conditions might not have shown a normal CO_2 response. However, the absence of a positive correlation meant that it was unlikely for physiological dysfunction at extreme temperatures to have accounted for the lack of stronger CO_2 enhancement.

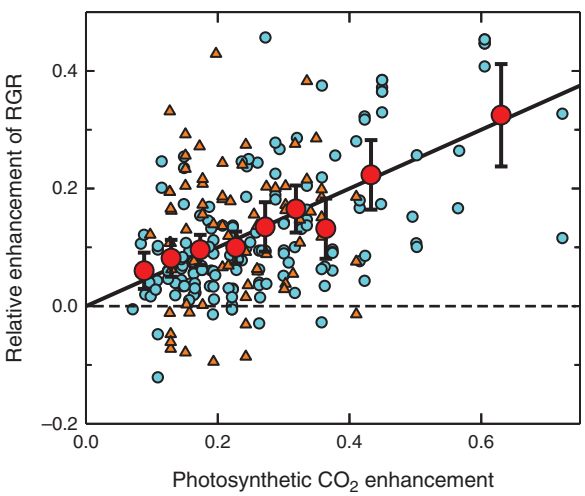

Fig. 4. Observed CO_2 enhancement of RGR, c_{enh}, plotted against calculated photosynthetic CO_2 enhancement. Shown are all observations (small symbols; $n = 238$) for herbaceous (circles) and woody species (triangles), and mean growth enhancement (large symbols) averaged over 0.05 intervals of photosynthetic enhancement. Error bars show 95% confidence intervals. The solid line was forced through the origin and fitted to the means, given by $c_{enh} = 0.495\ E_{low,high}$ ($r^2 = 0.94$; $P < 0.001$). This figure combines all data obtained for unstressed plants. A few individual data points were located outside the defined axis limits, but all data were included in the calculated averages.

Interactions with PAR

Fig. 7 shows RERC differences (ΔRERC) between plants grown at limiting and adequate PAR. Values on the *x*-axis show the extent to which RGR_{350} was reduced under low PAR, and values

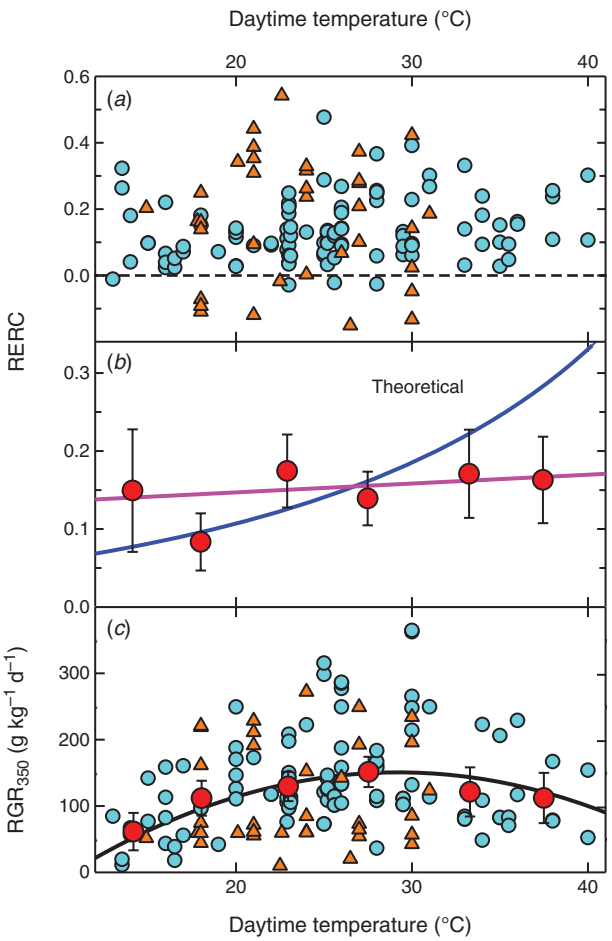

Fig. 5. (*a*) Relative enhancement of relative growth rate, RERC, (*b*) mean enhancement over different temperature intervals shown with 95% confidence intervals, and (*c*) RGR_{350}, the recorded relative growth rate under low [CO_2], all expressed against mean daytime temperature. Data from herbaceous species are shown as circles and data from woody species as triangles in (*a*) and (*c*). Data in (*b*) and the larger symbols in (*c*) were calculated over 5° temperature intervals. The blue line in (*b*) shows the theoretically expected RERC, based on the theoretical enhancement of photosynthesis (Eqn 4) and the empirical term of 0.495 obtained from the slope of the line in Fig. 4. The pink straight line in (*b*) is given by $RERC = 0.10 + 0.0019\ T$ ($r^2 = 0.24$; $P = 0.32$). The line in (*c*) is a polynomial fitted to the observations for better illustration of the trend. Mean RERC was 0.144 ± 0.021 for all data, with 0.136 ± 0.018 for herbs and 0.168 ± 0.062 for woody species.

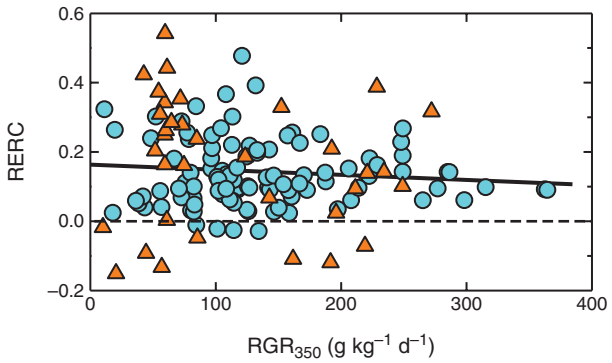

Fig. 6. Relative enhancement of relative growth rate by [CO_2], RERC, expressed as a function of RGR_{350} in different experiments. Symbols as for Fig. 5. The solid line has been fitted to the data, given by: RERC = 0.16 – 0.15 × 10^{-3} RGR_{350} (r^2 = 0.008; n = 140; P = 0.31).

on the *y*-axis show Δ*RERC* between plants grown under low and high PAR in the same experiment. If CO_2 responsiveness had been independent of the extent of PAR limitation, the data should have simply scattered around the *x*-axis without any trends with changing PAR limitations.

However, plants grown under severely limiting PAR displayed stronger CO_2 responsiveness than that observed under higher PAR levels. The difference in responsiveness was only slight for minor PAR limitations, with $g_{lim} > 0.8$, but for lower ratios, the effect became stronger and clearly apparent. For $g_{lim} < 0.8$, eight out of 10 observations showed higher CO_2 responsiveness under limiting than adequate PAR (Fig. 7).

Interactions with fertility

There was little fertility effect on ΔRERC for relative nutrient limitations >0.6, but the most severely stressed plants showed markedly reduced CO_2 responsiveness (Fig. 8). Three of the five experiments with $g_{lim} < 0.5$ even had calculated negative RERCs

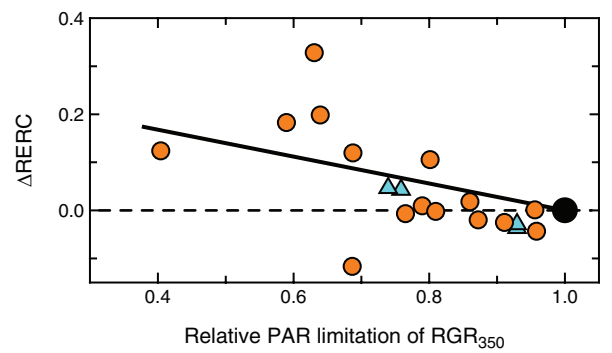

Fig. 7. ΔRERC plotted against the relative PAR limitation of RGR_{350} in different experiments. Data for each individual experiment were represented by the large black symbol at (1,0) to represent the normalised observation at high PAR, and one or more normalised points (smaller coloured symbols) at lower PAR characterised by a reduced RGR_{350} and a ΔRERC between that observed in low and high PAR. Symbols as for Fig. 5. The solid line was fitted to the data, forced through 0 at 1. ΔRERC = 0.28 – 0.28 g_{lim} (r^2 = 0.38; n = 19; P < 0.001), where g_{lim} is the relative PAR limitation of RGR_{350} (Eqn 8).

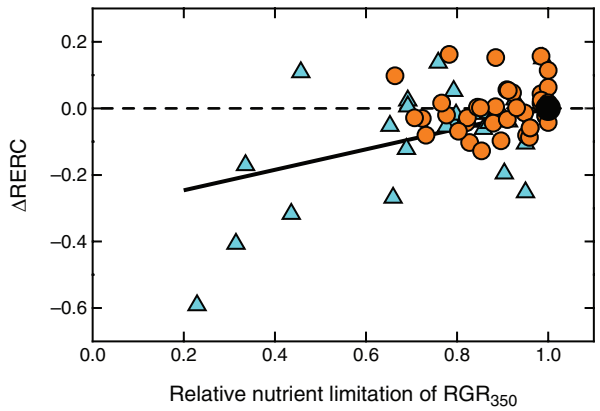

Fig. 8. ΔRERC plotted against relative nutrient limitation of RGR_{350} in different experiments. Data were calculated as outlined as for Fig. 7. Symbols as for Fig. 5. ΔRERC = –0.31 + 0.31 g_{lim} (r^2 = 0.30; n = 67; P < 0.001), where g_{lim} is the relative nutrient limitation of RGR_{350}.

(data not shown), which meant that their growth was actually reduced by exposure to elevated [CO_2].

Interactions with water stress

ΔRERC increased strongly under water stress, especially with $g_{lim} < 0.8$ (Fig. 9). The extent of ΔRERC was also quite pronounced. Under well watered conditions, RERC was only ~0.14 (cf. Fig. 5*b*), yet that was increased up to 3-fold when plants were water stressed (with g_{lim} <0.6).

Discussion

The present work focussed on analysing plant responses to elevated [CO_2] over the initial phase of exponential growth, but how relevant is the response over that short growth phase? Although the growth response of young plants is of some importance in itself, its greater relevance lies in providing an indication of likely plant responses during their longer and more relevant later linear growth phase. As a first approximation, one can quantitatively equate the relative enhancement of RGR (RERC) with an expected relative growth enhancement of linear growth. If that extrapolation can be made, these short-term experiments can provide valuable insights into the

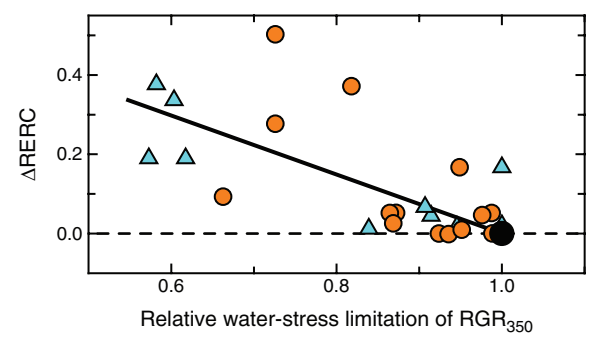

Fig. 9. ΔRERC plotted against relative water-stress limitation of RGR_{350} in different experiments. Data were calculated as outlined as for Fig. 7. ΔRERC = 0.74 – 0.74 g_{lim} (r^2 = 0.59; n = 24; P < 0.001), where g_{lim} is the relative water-stress limitation of RGR_{350}.

interactions between CO_2 responsiveness and other growth-limiting factors.

Although conditions in FACE experiments are such that plant responses can manifest themselves in the most natural way without artificial confounding factors (e.g. Ainsworth and Long 2005; Norby and Zak 2011), their costs and logistic challenges limit the extent to which interactions with other growth-limiting factors can be investigated (e.g. Pinkard *et al.* 2010). It is simply not feasible to conduct enough FACE experiments to gain sufficient insights either into species differences, or into all the possible interactions between plants' CO_2 responses and other growth-limiting factors.

Short-term and low-cost experiments in growth chambers and glasshouses can thus cost effectively add valuable insights to the overall understanding of the interactions between the key interacting factors. In the analysis of such experiments it is critically important, however, to be mindful of the positive feedback on growth during the exponential growth phase (Loehle 1995; Gifford *et al.* 1996; Körner 2006; Kirschbaum 2011). Biomass enhancement ratios (BERs) are inappropriate for expressing research results as the observed relative CO_2 enhancement is confounded by time so that a constant enhancement of RGR turns into an increasing BER with the length of experiments (Gifford *et al.* 1996; Fig. 1*c*). It is similarly confounded with the RGR of plants under normal $[CO_2]$, RGR_{350} (Fig. 2). Instead, a more generic measure of plant growth response to elevated $[CO_2]$ is the relative enhancement of RGR by elevated $[CO_2]$ (RERC). If needed, BERs can be easily calculated for specified combinations of RERC, RGR_{350} and time.

Quantifying differences in RERC made it possible to study interactions between the CO_2 response of young plants and temperature, PAR, fertility, and water stress without being confounded by the length of experiments or RGR_{350}. In plants grown under optimal conditions, RERC was independent of plants' RGR_{350} (Fig. 6), which is consistent with the findings by Poorter and Navas (2003), who had primarily compared species with different inherent growth potential. Fig. 6 showed that the same pattern also holds when differences in RGR_{350} were further increased by differences in experimental temperatures. As a first conclusion, fast- and slow-growing plants thus had the same RERC (Fig. 6), indicating a similar photosynthetic response and similar interaction with feedback processes. The reported differences in BERs between fast- and slow-growing plants reported in Table 1 resulted simply from differential amplification of the same underlying CO_2 response during the exponential growth phase (cf. Fig. 2).

Response to $[CO_2]$

Fig. 4 shows that it was possible to predict the growth response of plants to elevated $[CO_2]$ directly from the calculated enhancement of photosynthesis. Photosynthetic theory can be used to calculate the enhancement of photosynthesis for any combination of temperature and low and high $[CO_2]$ (e.g. Farquhar and von Caemmerer 1982; Kirschbaum 1994). This could be linked to the experimentally observed relative growth enhancement through the empirical constant 0.495 obtained from the slope of the straight line in Fig. 4. This tight correlation between calculated photosynthetic enhancement and observed growth enhancement thus provided an extremely useful approach for predicting the growth response of plants during their exponential growth phase.

The slope of 0.495 accounted for any changes in carbon use efficiency, specific leaf area, leaf mass fraction, or any possible reduction in photosynthesis in response to carbohydrate saturation under specific circumstances (Poorter and Navas 2003; Ainsworth and Long 2005). The correlation between photosynthesis and growth appeared to hold over a wide range of $[CO_2]$, with no indication of saturation at high $[CO_2]$ beyond that represented in the relevant photosynthetic equations. This provided an objective and quantitative way of accounting for the various feedbacks and secondary physiological and morphological responses that together determined the CO_2 response of plants.

At the same time, while there was a tight linear correlation between the average calculated photosynthetic enhancements and the observed growth enhancements, individual observations scattered widely around the mean response. Much of that scatter was simple random variation, given that it was often difficult to deduce the relevant parameters from sparse or noisy datasets. Additional deviation would have been related to temperature, which differed from the expected dependence (Fig. 5 and see below).

Differences between woody and herbaceous species, however, did not appear to add to the variability (Figs 4–6). However, there could have been other systematic differences in the response of different plants, such as between N-fixing and non-fixing plants, or other unspecified differences between species. Future data analyses to calculate differences in RERC could provide an effective way to search for further differences between species or functional groups.

Interactions with temperature

We found that on average, RERC was increased by $14 \pm 2\%$ when $[CO_2]$ was doubled, with the relative CO_2 responsiveness of plants being almost completely independent of temperature (Fig. 5). This contrasts with the findings by Poorter and Navas (2003; Table 1), who reported that BERs were lower for low-temperature grown plants. However, low temperatures are usually associated with reduced RGRs (Fig. 5*c*). The low BERs of low temperature-grown plants may have been a consequence of their lower RGRs that transformed invariant RERCs to lower BERs (Fig. 2).

However, it is difficult to reconcile the observed temperature-invariant RERC with the well-established interaction between temperature and photosynthetic CO_2 responses (e.g. Farquhar and von Caemmerer 1982). Photosynthesis in C_3 plants responds to $[CO_2]$ primarily because oxygen and CO_2 compete for the primary binding site on Rubisco, with increasing temperature favouring oxygenations. Hence, with increasing temperature, photosynthesis becomes increasingly limited by $[CO_2]$ at normal atmospheric concentrations (e.g. Farquhar and von Caemmerer 1982; Kirschbaum 1994; Medlyn *et al.* 2002). On the basis of that strong and universally observed photosynthetic relationship, a similar interaction was assumed to exist between temperature and the growth response to elevated $[CO_2]$ (e.g. Idso *et al.* 1987; Long 1991; Rawson 1992; Kirschbaum 1994; Polley 2002).

However, studies of growth responses to $[CO_2]$ under contrasting temperatures have provided ambiguous results. The early work reported by Idso *et al*. (1987), working with four different species, reported a strong $[CO_2] \times$ temperature interaction, but subsequent experiments produced more variable results. Rawson (1992) compared the strength of the $[CO_2] \times$ temperature interaction observed in various studies and concluded that, while there was greater CO_2 responsiveness at higher temperatures, it was only weakly and inconsistently expressed. Similarly, Morison and Lawlor (1999) summarised data from 106 different observations, covering 18 different species, and found only a weak $[CO_2] \times$ temperature interaction. A recent meta-analysis of experiments with increased temperatures and $[CO_2]$ also found little support for a $[CO_2] \times$ temperature interaction in whole-plant growth responses (Wang *et al*. 2012).

These earlier studies, together with the very weak $[CO_2] \times$ temperature interaction observed here, indicate that the $[CO_2] \times$ temperature interaction that is clearly apparent in photosynthetic responses does not carry over into whole-plant growth responses. However, there are no obvious reasons for the absence of greater growth enhancements at higher temperatures. It could have been possible that plants experiencing extremely high or low temperatures might not have functioned normally and therefore been unable to utilise the extra carbohydrate made available through elevated $[CO_2]$. However, there were only moderate reductions in RGR_{350} at even extreme temperatures (Fig. 5*c*), and there was no indication of reduced CO_2 responsiveness for the slowest-growing plants (Fig. 6). Thus, there was no evidence of physiological dysfunction to have prevented plants from utilising an enhanced carbohydrate supply.

An uncoupling of photosynthesis and growth is often associated with the assumption that plants might be sink- rather than source-limited (e.g. Millard *et al*. 2007; Kirschbaum 2011). If plants already have excess carbohydrate resources under normal $[CO_2]$, it would be unlikely for their growth to be enhanced by elevated $[CO_2]$, even if short-term photosynthetic rates could be increased. However, plants are more likely to be sink-limited under cooler conditions (Poorter *et al*. 2013) when maintenance respiration and growth processes might be slowed by low temperatures. This could lead to sink limitation that could hypothetically prevent a CO_2 response. In contrast, higher temperatures should stimulate respiration and growth processes (e.g. Atkin and Tjoelker 2003; Way and Yamori 2014), deplete carbohydrate reserves, and shift plants from sink to source limitation. High temperatures should create conditions favourable for full utilisation of increased photosynthetic carbon gain, and carbohydrate feedbacks should have further enhanced the $[CO_2] \times$ temperature interaction, rather than negated it. These considerations thus can provide no explanation for the absence of the expected $[CO_2] \times$ temperature interaction.

It is difficult to think of other possible explanations for this intriguing absence of the expected response pattern. However, whatever the cause for the absence of a $[CO_2] \times$ temperature interaction, it has profound implications for the modelling of plant responses to changes in future $[CO_2]$.

Interactions with PAR limitations

The analysis showed that low PAR-grown plants were more responsive to elevated $[CO_2]$ than plants grown under high PAR (Fig. 7). Plant growth could be more responsive to $[CO_2]$ under PAR limitation because plants operate closer to their light-compensation point, and because PAR-limited plants are likely to be carbohydrate limited so that enhanced photosynthesis would convey greater advantages than for plants grown under higher PAR. In contrast, an analysis based on BERs had shown low- and high PAR-grown plants to be similarly responsive to elevated $[CO_2]$ (Table 1; Poorter and Navas 2003). So, as for other interactions presented here, it is likely that the actual greater RERC under low PAR was masked by the reduction of BERs through lower RGR_{350} in the plants grown under limiting PAR (cf. Fig. 2).

Greater CO_2 responsiveness of PAR-limited plants might be a factor contributing to the increasing density of rainforest lianas that has been observed over recent decades (e.g. Phillips *et al*. 2002; van der Heijden *et al*. 2013). Lianas typically start their growth under PAR-limited conditions in the forest understorey. Greater CO_2 responsiveness would thus allow them to take greater advantage of increasing $[CO_2]$ than the over-storey trees with which they compete. This could give lianas a competitive boost that might contribute to their increasing abundance.

Interactions with nutrient limitations

CO_2 responsiveness was reduced under nutrient-limited conditions, but the trend was weak and only readily apparent in studies with severe nutrient limitations (Fig. 8). However, it was difficult to analyse CO_2 responses under nutrient-limited conditions with the approach adopted here because different nutrient levels were commonly set by applying different amounts of fertiliser at the start of experiments. For the youngest plants, those amounts could have been adequate for growth (cf. Ingestad and Lund 1986; Poorter *et al*. 2012) so that initial RGRs did not differ markedly between high- and low fertility-grown plants, which led to the majority of observations being bunched together with relative growth limitations ≥ 0.8 and similar CO_2 responsiveness. More substantial growth responses often developed at later growth stages, but those downturns had little effect on the inferred initial relative growth rates. The present findings therefore relied on only a very small number of observations where the fertility constraints were imposed in such a way that RGRs were affected from the earliest growth stages.

However, although our study provides a less certain answer as to how far nutrient limitations curtailed CO_2 responses at the plant-physiological level, it is likely that under long-term conditions in the field, feedbacks through whole-system nutrient availability strongly interact with the CO_2 response of plant growth. Plants and soils have confined C : N ranges, and any increased carbon gain through elevated $[CO_2]$ is ultimately curtailed by the need to also obtain nitrogen so that C:N ratios can be maintained within their allowable ranges. This should reduce the CO_2 responsiveness under nutrient-limitations compared with that of well fertilised plants. This feedback effect has been observed experimentally (e.g. Norby *et al*. 2010; McCarthy *et al*. 2010) and in modelling studies (e.g. Comins and McMurtrie 1993; Kirschbaum *et al*. 1998). While these constraints have been investigated primarily with respect to

C : N ratios, similar, although more complex, relationships also hold for phosphorus and sulfur (Kirschbaum *et al*. 1998).

Interactions with water-stress limitations

CO_2 responsiveness strongly increased in water-stressed plants (Fig. 9). This response was consistent and apparent in all plants with a water-stress limitation of 0.9 or lower. The response was also numerically strong, giving an approximate 3-fold increase in CO_2 responsiveness from unstressed to the most severely stressed plants. When plants are water-stressed, growth limitations shift from photosynthesis that shows only moderate CO_2 sensitivity to limitation by water-use efficiency, for which greater CO_2 responsiveness can be expected (e.g. McMurtrie *et al*. 2008). However, just as for fertility experiments, water stress in most experiments was imposed in such a way that it only marginally affected early plant growth so that the analysis had to rely on few usable observations, but those data showed strongly increased CO_2 responsiveness under water limitation.

On the other hand, the pattern of increasing CO_2 responsiveness under water-limited conditions is not consistently observed in FACE experiments (Kimball *et al*. 2002; Nowak *et al*. 2004; McCarthy *et al*. 2010), not even in desert environments, where one might expect a strong and consistently enhanced CO_2 response (e.g. Newingham *et al*. 2013). It is thus not certain to what extent the findings from the short-term studies reported here are consistently expressed under field conditions, or, if they are not, what higher-order interactions prevent their expression under field situations.

General points

Despite much research over many years, there is still uncertainty about the growth response of plants to elevated [CO_2] (e.g. Reddy *et al*. 2010; Wang *et al*. 2012). This is partly due to the complex interactions between the photosynthetic CO_2 response and the numerous other factors that together control plant growth. Plant growth not only provides the ultimate sink for photosynthetically fixed carbon, but can also exert a strong feedback control on photosynthetic carbon gain to ensure a balance between photosynthetic carbon gain and its use in growth (e.g. Paul and Foyer 2001). The photosynthetic response to changing [CO_2] can therefore only be fully understood if growth processes are simultaneously considered as well.

Understanding these interactions is challenging and demands experimental work in which different co-limitations can be varied together with changes in [CO_2]. Short-term experiments conducted in growth chambers or glasshouses provide a cost-effective and feasible approach to generating the data for a better understanding of these important interactions. However, studies during the plants' exponential growth phase need to be analysed in such a way to generate generic and unconfounded growth indices that are comparable between different growth conditions and between different experiments. The present work used a novel approach by calculating the relative enhancement of plants' relative growth rate during the initial growth phase. As a first approximation, that relative enhancement of RGR can also be used for predicting growth responses during the plants' subsequent linear growth phase.

Overall, the present work illustrated that useful information can be obtained from short-term growth-chamber or glasshouse-based studies. However, the key is that the analysis must separate the inherent CO_2 response of plants from its amplification during the exponential growth phase. This made it possible to obtain the range of observations needed for better quantification of the CO_2 response of plants, and disentangle the direct CO_2 response from its various important co-limiting factors.

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