Comment

Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO_2?

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Abstract

Mainly based on a simulation model, Lloyd & Farquhar (1996; *Functional Ecology,* 10, 4-32) predict that inherently slow-growing species and nutrient-stressed plants show a relatively strong growth response to an increased atmospheric CO_2 concentration. Compiling published experiments, I conclude that these predictions are not supported by the available data. On average, inherently fast-growing species are stimulated proportionately more in biomass than slow-growing species and plants grown at a high nutrient supply respond more strongly than nutrient-stressed plants.

Recently, Lloyd & Farquhar (1996) published a model to analyse the effect of elevated atmospheric CO_2 concentrations on plant growth. Starting with the Farquhar model on photosynthesis, and adding equations for growth and maintenance respiration as well as nitrogen uptake, they analysed plant responses at a range of scales, from leaf to ecosystem. Such a model as a simplification of a complex reality can help to guide one's mind. However, in their comparison between model output and experimental data, I consider that Lloyd & Farquhar (1996) make some statements, which may confuse the issue. In this forum, I discuss two of them.

Fast- and slow-growing species

Based on their model, Lloyd & Farquhar (1996) predict that plants with a relatively high fraction of daily fixed photosynthate respired again during the same day ('ϕ' in their paper) will respond more strongly in terms of growth than those with a low ratio of respiration to photosynthesis. Therefore, they expect that species with a low potential growth rate, which generally have a higher ϕ (Van der Werf *et al.* 1994), will show a higher enhancement ratio (mass of plants grown at a high [CO_2] divided by the mass of plants at control levels of CO_2) than those with a high potential growth rate. This contradicts

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evidence presented in the literature (compiled in Poorter 1993, updated in Poorter *et al.* 1996). Lloyd & Farquhar (1996) take issue with these data and suggest that the analysis of the data was incorrect. First, they note that the highest and lowest enhancement ratios observed within each category of plants were excluded. Secondly, they - implicitly - doubt the application of a logarithmic transformation prior to analysis of ratios. Thirdly, they conclude that there is no significant difference between fast- and slow-growing species as the enhancement ratios of crop and herbaceous wild plants, re-analysed in their way, show a probability of being similar between 0.05 and 0.10.

On the first point, one has to be aware that enhancement ratios show a high degree of variability, as both the numerator and the denominator are estimated values. Variability in each of these terms will depend on variability of the population of plants under investigation and the number of plants harvested per treatment. In the 'average' experiment, confidence limits for enhancement ratios are quite wide (reviewed in Poorter *et al.* 1996), which implies a high risk of outlying observations. Moreover, unrecognized errors in the compiled dataset could occur anywhere in the process from carrying out the experiment to extracting data from the literature. In my opinion, it is better to use a 'trimmed' mean, calculated after systematically excluding the highest and lowest values in each category of interest. Such a trimmed mean is a robust estimator of location (Norusis 1993, p. 192),

Table 1 Mean enhancement ratios (plant mass at 600-800 μmol mol^{-1} CO_2 divided by plant mass at 300-400 μmol mol^{-1} CO_2) of various types of herbaceous C3 species (after Poorter et al. 1996). Compilation of literature data on individually grown plants in the vegetative phase. Wild species were classiefied as being fast-, intermediate- or slow-growing on the basis of comparative growth experiments, or on the basis of information on life-history and soil fertility in their natural habitat. All ratios were logarithmically transformed prior to averaging

Functional type	Number of species	Enhancement ratio
Crop species	23	1.58
Wild species		
High RGR	30	1.60
Intermediate RGR	36	1.43
Low RGR	42	1.27

providing a better impression of the main body of literature data.

Second, ratios are not normally distributed (Sokal & Rohlf 1995, p. 18). A simple thought experiment may serve as illustration. Let us assume results of two experiments, one in which the high CO_2-grown plants were 2 gram and the controls 1 gram (enhancement ratio = 2), and one experiment in which it was the other way around (enhancement ratio = 0.5). The conclusion based on these two experiments has to be that there is no effect of [CO_2]. However, calculating the average enhancement ratio, as advocated by Lloyd & Farquhar (1996), results in a value of 1.25, implying that there was an average growth stimulation of 25%. If, prior to averaging, a ln-transformation was carried out on the enhancement ratios (yielding 0.69 and -0.69), and the mean value would be back-transformed afterwards to the original scale, the mean enhancement ratio would have been 1. This indicates no average growth stimulation, which indeed is the unbiased estimate of the overall response.

Third, Lloyd & Farquhar (1996) reanalyse the compiled data set to cast doubt on the conclusion that fast-growing species respond more strongly than slow-growing species. They do so by comparing all crop species with all herbaceous wild species. However, the group of herbaceous wild species is rather heterogeneous, with some species growing as fast as or faster than crops, and others growing much slower. Thus, the relevant test would be to compare species with different growth rates. When this is done, fast-growing wild species and crop species show similar growth stimulations, whereas the inherently slow-growing ones have, on average, a much lower response ($P < 0.001$; Table 1). Based on their model, Lloyd & Farquhar (1996) predict slow-growing species to have higher enhancement ratios. I contend that this is not supported by experimental evidence.

CO_2 response at low nutrient supply

Bazzaz (1990) concluded that nutrient-limited plants respond less to increases in atmospheric CO_2 than plants grown at a high nutrient availability. Lloyd & Farquhar (1996) claim that there is neither theoretical nor experimental evidence for this contention. However, I do think there are theoretical considerations. Low-nutrient plants consistently show accumulation of nonstructural carbohydrates in the leaves (Chapin 1980). Obviously, growth is limited to a greater extent than photosynthesis (Chapin 1980; Körner 1991). The primary effects of increased carbon dioxide are an increase in photosynthesis and a decrease in transpiration. In the case of nutrient-stressed plants this will imply an even greater production of sugars that cannot be converted to structural growth, whereas on the other hand the mass flow of ions like nitrate to the roots will be reduced, and consequently ion uptake. It is difficult to envisage a strong response of such plants to elevated [CO_2].

Are these theoretical expectations supported by experimental evidence? As noted by Lloyd & Farquhar (1996, their table 1) outcomes are rather variable with both increases and decreases in enhancement ratios. There may be several reasons for such variability. First, Lloyd & Farquhar (1996) have compiled papers with a mix of experimental approaches. Several of their observations are from interspecific competition experiments, where changes in biomass at low nutrient availability may be due to indirect effects by one of the competing species. Other observations deal with experiments in which plants were grown individually, but only shoot biomass was determined. Especially at low nutrient supply, CO_2 responses may be different for roots and shoots (Stulen & Den Hertog 1993). Thus, considering whole plant responses only is better. Secondly, nutrient limitation experiments are carried out in a variety of ways (plants grown in pots or in hydroponics, levels administered dependently or independently of plant size, type and form of nutrient, duration of the experiment). This may result in different limitations on plant growth, and differences in the relative response to elevated [CO_2] as well (e.g. Brown 1991). Thirdly, variability in the plant population in combination with relatively small sample sizes may be a reason, as outlined above. This is even more of a problem as *two* ratios are compared. Finally, a biological reason for the observed variability is that species may differ in their secondary responses to [CO_2]. Such a response can be a reduction in the synthesis of RUBISCO, or an increased investment in roots or mycorrhiza, implying a higher uptake of nutrients. These effects may allow for some extra N to be invested in what really forms the growth-limiting factor and subsequently a larger growth response (for an extended discussion see Rogers et al. 1996).

Given the above considerations on variability, I think that an assessment of the $CO_2 \times$ nutrient effects can only be made by a quantitative analysis of a large number of studies: what is the mean response over experiments published so far and what is the variation around the mean? To this end I compiled the literature on plant species grown individually in a factorial design of high/low [CO_2] and high/low nutrient-availability. The severity of nutrient stress varied between experiments, with sometimes only a marginal growth reduction, sometimes growth reductions of more than 90%. Any shift in the enhancement ratio is more likely to happen at severe nutrient stress. To account for that, enhancement ratios were plotted on the y-axis against the severity of the nutrient stress on the x-axis (Fig. la). The latter parameter was calculated by dividing the plant mass at low nutrient and low [CO_2] by that of plants grown at high nutrient and low [CO_2]. Enhancement ratios for the high nutrient treatment were plotted at $x = 1$. Data are variable and in some cases [CO_2] still stimulates growth at low nutrient availability to a considerable extent. However, as the question is whether there is a *decrease* in the enhancement ratio with decreasing nutrient availability, it is more appropriate to consider the slope of the regression line that fits data on different nutrient treatments within a species and within an experiment. In total I compiled 87 datasets. The distribution of their slopes is shown in Fig. 1b. On average the slope is positive (10% trimmed mean = 0.20; $P < 0.001$), indicating a lower CO_2 response at lower nutrient availabilities. However, variation is large and 26% of the calculated slopes is negative, be it generally close to zero. The extreme negative (< -0.1) and positive (> 0.5) values are most likely due to sampling variation. If so, my conclusion is that on average enhancement ratios decrease, but that in quite a number of cases they do not change with decreasing nutrient availability. Apparently, Bazzaz (1990) and Lloyd & Farquhar (1996) cover opposite sides of the same coin.
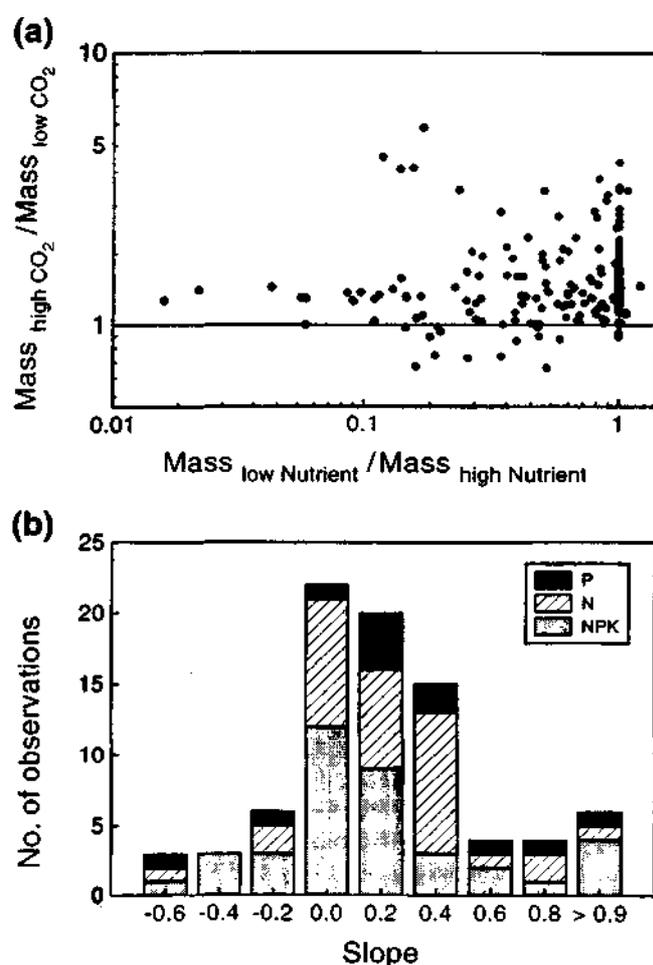

Fig. 1. (a) Enhancement ratios (mass at high [CO_2]/mass at low [CO_2]) of 87 data sets in which plant species were grown at high and low levels of nutrient availability. To account for variation in severity of the nutrient stress across experiments enhancement ratios were plotted against the ratio of biomass for the low-nutrient and the high-nutrient supply plants at control levels of [CO_2]. As ratios are log-normally distributed, axes are logarithmic. (b) Distribution of slopes of the regression lines fitted through the enhancement ratios of each of the 87 data sets plotted in (a). A distinction was made between experiments in which N ($n = 36$), P ($n = 12$) or nutrients in general (NPK; $n = 39$) were varied. No significant differences were found in the average slope between the three types of nutrient limitation. With a 10% trimmed mean for the slope of 0.20 (0.28 on average for all observations), a growth stimulation by elevated CO_2 of 50% at full nutrient supply turns into 0% stimulation when biomass would be reduced by 87% due to the low nutrient treatment.

Only those experiments were included in which total plant biomass was reported on individually grown, vegetative plants. Data sets where plants of the lowest nutrient treatment differed less than 10% in mass from plants of the highest nutrient treatment were discarded, as slopes could not be calculated with enough precision. In most cases (90%) the CO_2 concentration was roughly doubled (300-400 µmol mol^{-1} vs. 600-800 µmol mol^{-1}) and only in a few cases 'high CO_2 was as low as 550 µmol mol^{-1} or as high as 1500 µmol mol^{-1}. Data are from 53 publications: Sionit *et al.* (1981), Williams *et al.* (1981), Brown & Higginbotham (1986), Conroy & Barlow (1986), Conroy *et al.* (1988), Conroy *et al.* (1990), Israel *et al.* (1990), Conroy *et al.* (1992), Sritharan *et al.* (1992), Barett & Gifford (1995), Curtis *et al.* (1995), Griffin *et al.* (1995), Hunt *et al.* (1995), Johnson *et al.* (1995), Midgley *et al.* (1995), Pregitzer *et al.* (1995), Silvola & Ahlholm (1995), Townend (1995), Bowler & Press (1996), Gebauer *et al.* (1996), Newberry & Wolfenden (1996), Volin & Reich (1996), Chen & Lenz (1997), Griffin *et al.* (1997), Heath & Kerstiens (1997), Jablonski (1997), Prior *et al.* (1997), Whitehead *et al.* (1997) and E. Garnier, M.L. Navas & R. Gifford, (unpubl.), as well as from 25 papers listed in fig. 7 of Poorter *et al.* (1996).

However, the prediction of Lloyd & Farquhar (1996) that enhancement ratios are higher at low N-availability is not supported by the data.

It would be a major achievement if we understood why some plant species do not decrease their enhancement ratio at low nutrient availability, whereas most do. Whether the current photosynthesis-based models may help to clarify this point remains to be seen. My opinion is that plant growth at low nutrient supply or a high $[CO_2]$ is not constrained by C-availability and real understanding of their effect on growth has to be sought outside the domain of carbon budgets.

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