A Quantitative Analysis of Dark Respiration and Carbon Content as Factors in the Growth Response of Plants to Elevated CO₂

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Abstract

An analysis of elevated CO_2 effects (2-4 times ambient) on dark respiration rate and carbon content was undertaken for a wide range of plant species, using both published reports and new data. On average, leaf respiration per unit leaf area was slightly higher for plants grown at high CO_2 (16%), whereas a small decrease was found when respiration was expressed on a leaf weight basis (14%). For the few data on root respiration, no significant change due to high CO_2 could be detected. Carbon content of leaves and stem showed a small increase (1.2 and 1.7% respectively), whereas C-content of roots was not significantly affected. In both data sets direction of responses was variable. A sensitivity analysis of carbon budgets under elevated CO_2 identified changes in respiration rate, and to a lesser extent carbon content, as important factors affecting the growth response to elevated CO_2 in quite a number of cases. Any comprehensive analysis of growth responses to increased CO_2 should therefore include measurements of these two variables.

Introduction

Effects of high ambient CO_2 concentrations on plant growth are well established. On average, a doubling in the present atmospheric CO_2 concentration results in a stimulation of vegetative biomass of whole plants of 35% (Poorter 1992) and a similar stimulation is found for (marketable) yield (Kimball 1983). The primary cause of this growth stimulation is an increased rate of photosynthesis, partly due to suppression of photorespiration, partly due to a higher substrate level (Farquhar and von Caemmerer 1982). However, an increased supply of photosynthates may result in a number of secondary effects as well, such as alterations of specific leaf area (leaf area : leaf weight ratio), biomass allocation, respiration, and/or carbon content. Secondary changes may also occur due to a decreased stomatal conductance (Morison 1985).

How do both the primary and secondary changes due to a high CO_2 concentration affect growth? In their simplest form, growth on one hand, and carbon gain and carbon losses on the other, can be integrated by the following formula (Poorter and Welschen 1992):

$$RGR = \frac{[PS_a * SLA * LWR] - [LR * LWR + SR * SWR + RR * RWR]}{LCC * LWR + SCC * SWR + RCC * RWR} \quad , \quad (1)$$

where RGR is the relative growth rate of the plant (g g⁻¹ day⁻¹), PS the rate of photosynthesis per unit leaf area (mol C m⁻² day⁻¹), SLA the specific leaf area (m² g⁻¹), LWR the leaf weight ratio (leaf weight: total plant weight; g g⁻¹), SWR the stem weight ratio (stem weight:total plant weight), RWR the root weight ratio (root weight:total plant weight), LR, SR and RR the rate of respiration of leaves, stem and root respectively, expressed per unit organ weight (mol C g⁻¹ day⁻¹), and LCC, SCC and RCC the carbon content of leaves, stem and roots respectively (mol C g⁻¹).

To our knowledge, no experiments have as yet been published in which the effect of high CO_2 has been analysed for all the terms of equation (1). Photosynthesis and biomass allocation have received a lot of attention (for reviews see Pearcy and Björkman 1983; Stitt 1991; Stulen and Den Hertog 1992), but effects of long-term CO_2 enrichment on respiration and carbon concentration are poorly documented. Recently, Amthor (1991) and Ryan (1991) suggested a number of ways whereby high CO_2 could affect components of plant respiration. However, they did not make a quantitative analysis of effects of high CO_2 concentrations on respiration and possible consequences for growth. Documentation of effects of high CO_2 concentrations on C-content of plants is virtually absent. The aim of this paper is to explore the possible significance of both respiration and carbon content in explaining the growth stimulating effect of high CO_2.

Materials and Methods

Data on respiration rates and C-content were obtained from the literature, and supplemented with some yet unpublished results. All plants from our own experiments were grown at 350 and 700 μmol mol^{-1} CO_2. At harvest they were separated into leaves, stems and roots, and either oven-dried or freeze-dried. C-content was determined on ground material with a Carlo-Erba elemental analyser (Milan, Italy).

CO_2 effects on respiration rates and carbon content were analysed by calculating the ratio of values at high CO_2 compared with normal ambient levels. Such ratios do not follow a normal distribution. To correct for this, average values per species or per group of species are based on ln-transformed values of the ratios. In cases where the variable of interest was determined several times during the experiment on the same species, we averaged all the observed ratios. For convenience, these averages are back-transformed to normal values for inclusion in the tables. Data were analysed with the SAS statistical package (Joyner 1985). Before calculating the average value for each variable, we discarded the 10% lowest and the 10% highest values, to minimise the influence of outlying observations. In all cases, plants were grown at high and normal ambient CO_2 concentrations for relatively long periods of time (in general more than 20 days). Consideration was limited to enrichment studies where CO_2 did not exceed 1500 μmol mol^{-1}.

Results and Discussion

Respiration

One important issue in analysing respiration is the basis on which data should be expressed. CO_2 enrichment may cause considerable accumulation of starch (Farrar and Williams 1991), which is relatively inert from a physiological point of view. In assessing the effects of a high CO_2 concentration on physiology, this has led authors to avoid a dry weight basis. Thus, data have been expressed per unit leaf area (e.g. Oechel and Strain 1985) or, even better, on the basis of starch-free dry weight (e.g. Wong 1990). Since the latter procedure is only rarely adopted, we will consider ratios of leaf respiration on a leaf area basis. As we are concerned with the effect of respiration on whole plant growth as well, values are also expressed on a weight basis. Data have been listed for shoot and root respiration separately. In cases where whole plant respiration was either measured, or could be inferred from component values for shoot respiration, root respiration and biomass allocation, these data are given as well. However, a change in whole plant respiration is not necessarily caused by a change in the respiration rate of the various plant organs, but might also be brought about by a shift in biomass allocation. Therefore, we will concentrate on the rates for the various organs.

Ratios of leaf, root and whole plant respiration at different CO_2 concentrations are listed in Table 1. Their frequency distribution is given in Fig. 1. Leaf respiration per unit leaf area shows wide variation, ranging from over 50% inhibition under high CO_2 to more than 200% stimulation (Fig. 1*A*). On average a significantly higher respiration rate is found in this data set for high CO_2 plants *(P < 0.001)*. Ratios for leaf respiration expressed per unit leaf weight

Table 1. Ratio of the respiration rate of plants grown at high and at control CO_2 concentrations
Respiration rates on which the ratios are based are expressed either per unit leaf area (/area) or per unit dry weight of that organ or total plant (/DW). In some cases respiration given under 'leaf was actually determined on whole shoots. Data on leaf respiration of *Pisum sativum* were reported on a fresh weight basis only, but as the LA/FW ratio of enriched and control plants are more comparable than FW/DW ratios, we have listed these data under respiration per LA. Average values per category are given after removing the 10% smallest and 10% largest observations in each category. *P* gives the probability that the ratio does not differ from 1. +, $0.05 < P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Species	CO_2 concn (μmol mol^{-1})		Respiration ratio				Reference
			Leaf /area	Leaf /DW	Root /DW	Plant /DW	
C_3 species							
Acacia mangium	350	700	0.77	0.71			L.H. Ziska, unpublished
Acer saccharinum	350	700				0.65	Bunce 1992
Agrostis capillaries	340	680	1.06				Williams *et al.* 1992
Beta vulgaris	330	1000	1.51				Ford and Thome 1967
Betula nana	350	675	1.35				Oechel and Strain 1985
Carex bigelowii	350	675	1.80				Oechel and Strain 1985
Chrysanthemum morifolium	325	1500				0.69	Hughes and Cockshull 1972
Citrus aurantium	350	650	0.63				Idso and Kimball 1992
Dactylis glomerata	350	700				0.80	Bunce and Caulfield 1991
Eichhornia crassipes	330	600				0.59	Spencer and Bowes 1986
Eriophorum vaginatum	350	675	0.98				Oechel and Strain 1985
Ficus obtusifolia	350	700	0.99	0.80			L.H. Ziska, unpublished
Glycine max	350	1000	0.95	0.98			Imai and Murata 1978
	350	700	1.28	1.00		0.91	Bunce 1990
	350	1000	1.41	1.22			Hrubec *et al.* 1985
Gossypium hirsutum	350	650	1.31				Harley *et al.* 1992
Helianthus annuus	340	680			1.26		Gifford *et al.* 1985
Hordeum hexastichum	350	1000	1.12	1.01			Imai and Murata 1978
Hordeum vulgare	350	700	1.69				Williams *et al.* 1992
	300	1000	1.03				Ford and Thome 1967
Ledum palustre	350	675	1.52				Oechel and Strain 1985
Liriodendron tulipifera	376	676	0.63	0.52			Wullschleger *et al.* 1992
Lolium perenne	350	700				0.58	Bunce and Caulfield 1991
	350	625	1.95				Nijs and Impens 1992
	340	680	1.36	0.98		0.94	Ryle *et al.* 1992
Lycopersicon esculentum	350	700	0.88	0.78		0.82	Bunce 1990
	300	1000	0.89				Woodrow and Grodzinski 1987
	300	800	1.34				Hicklenton and Joliffe 1978
	300	1000	1.55				Hicklenton and Joliffe 1980
	350	1000	1.55	1.30			Ho 1978
Malus domestica	350	700				0.61	Bunce 1992
Manihot esculentua	350	700	0.54	0.50			L.H. Ziska, unpublished
Medicago sativa	350	700				0.66	Bunce and Caulfield 1991

Table 1 *(continued)*

Oryza sativa	350	1000	0.92	1.16			Imai and Murata 1978
	330	660		1.07			Baker *et al.* 1992
	330	900		0.96			Baker *et al.* 1992
	360	660	0.52	0.45			Ziska and Teramura 1992
	360	660	0.71	0.65			Ziska and Teramura 1992
Pharus latifolia	350	700	1.32	1.36			L.H. Ziska, unpublished
Pisum sativum	350	650	0.86				Musgrave *et al.* 1986
	350	650	1.40				Musgrave *et al.* 1986
	350	650	1.24				Musgrave *et al.* 1986
Plantago major	350	700	1.25	1.03	1.27	1.06	Poorter *et al.* 1988
ssp. *major*	350	700			0.97		H. Poorter, unpublished
Plantago major	350	700	2.37	2.05	0.99	1.74	Den Hertog *et al.* 1992
ssp. *pleiosperma*							
Poa alpina	340	680	1.43				Williams *et al.* 1992
Psychotria limonensis	350	700	0.93	0.75			L.H. Ziska, unpublished
Quercus alba	376	676	0.43	0.41			Wullschleger *et al.* 1992
Quercus prinus	350	700				0.47	Bunce 1992
Scirpus olneyi	351	680	1.00				Long and Drake 1991
Tabebuia rosea	350	700	0.81	0.54			L.H. Ziska, unpublished
Trifolium repens	367	620				0.87	Nijs *et al.* 1988
Triticum aestivum	350	1200	1.16				Kendall *et al.* 1985
	340	680			0.55		Gifford *et al.* 1985
	340	680			0.92		Gifford *et al.* 1985
Urtica dioica	350	700				1.04	Jansen *et al.* 1986
	350	700			0.94		H. Poorter, unpublished
Vaccinium uliginosum	350	675	2.21				Oechel and Strain 1985
Vaccinium vitis-idaea	350	675	2.69				Oechel and Strain 1985
Vigna radiata	340	680			0.80		Gifford *et al.* 1985
Mean value C₃			1.140	0.849	0.972	0.767	
P			**	+		***	

C₄ species

Amaranthus hypo-chondriacus	350	700	0.94	0.98		0.98	Bunce 1990
Echinochloa crus-galli	350	675	1.21				Potvin and Strain 1985
	350	675	1.58				Potvin and Strain 1985
	350	675	1.99				Potvin and Strain 1985
Echinochloa frumentacea	350	1000	1.30	1.20			Imai and Murata 1978
Eleusine indica	350	675	1.44				Potvin and Strain 1985
Paspalum conjugatum	350	700	0.69	0.74			L.H. Ziska, unpublished
Zea mays	350	1000	1.05	0.94			Imai and Murata 1978
Mean value C₄			1.233	0.941		0.980	
P			*				
Mean value C₃ and C₄			1.156	0.863	0.972	0.783	
P			***	*		**	

are lower (Fig. 1*B*), due to a decrease in the leaf area:leaf dry weight ratio under elevated CO_2. On average, high CO_2 plants respire somewhat less than control plants *(P < 0.05)*. It should be borne in mind that the two data sets on leaf respiration partly consist of different experiments. Root respiration seems less affected by high CO_2, although variability in reported values is considerable, values ranging from a 45% inhibition to a 30% stimulation (Fig. 1*C*).
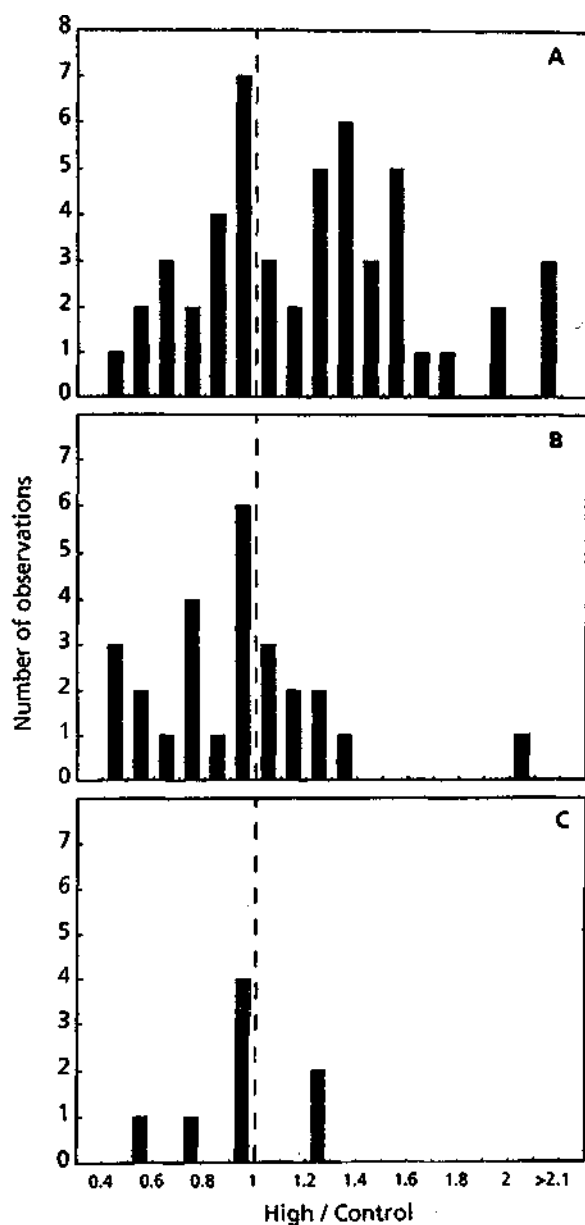

Fig. 1. Distribution of the observed ratios in respiration of high CO_2 and control grown plants. Data are taken from Table 1.
(*A*). Leaf respiration (or shoot respiration) per unit leaf area.
(*B*). Leaf respiration (or shoot respiration) per unit leaf dry weight (or per unit shoot dry weight).
(*C*). Root respiration per unit root dry weight.

What causes this wide variation in response to CO_2 enrichment?

First, technique may contribute, because respiration is measured as either O_2 consumption or CO_2 evolution, at different periods during the diurnal cycle, with or without soil, and with ambient CO_2 concentrations which sometimes differed from those during growth.

Second, in most reports respiration is only measured once. In the few cases where respiration was measured on several occasions during development or on various tissues, important variations were observed. For example, Hrubec *et al.* (1985) found respiration in young leaves of high-CO_2 grown soybeans to be higher than those grown at normal CO_2, but this stimulation did not occur in older leaves. Poorter *et al.* (1988) found a clear time dependence in the effect of high CO_2 on respiration of *Plantago major* ssp. *major* (Fig. 2), especially in the roots. The low rates of respiration at high CO_2 concentration during growth in salt marsh species occurred only later in the season (B.G. Drake, personal communication). Therefore, part of the variation in response may be attributable to ontogeny.

Finally, high CO_2 may affect components of respiration differently in different species, or under contrasting circumstances. Respiration has been subdivided into components related to growth (growth rate and specific costs for growth), maintenance and, for roots, nutrient uptake (nutrient uptake rate and specific costs for the uptake of ions; Van der Werf *et al.* 1989). Whilst the growth rate of plants is (temporarily) enhanced by high CO_2, the specific costs of growth (in terms of CO_2 produced or O_2 consumed per gram of newly formed plant material) may decrease, owing to the accumulation of energetically 'cheap' sugars. The increase in non-structural carbon may also cause the maintenance costs per gram dry weight to go down. Similarly, the costs of uptake of nutrients (on a plant mass basis) may decrease. The net result of all these changes could be a decrease in respiration in some cases, but an increase in others, depending on how each of these components is affected. For a more thorough discussion see Amthor (1991) and Ryan (1991).
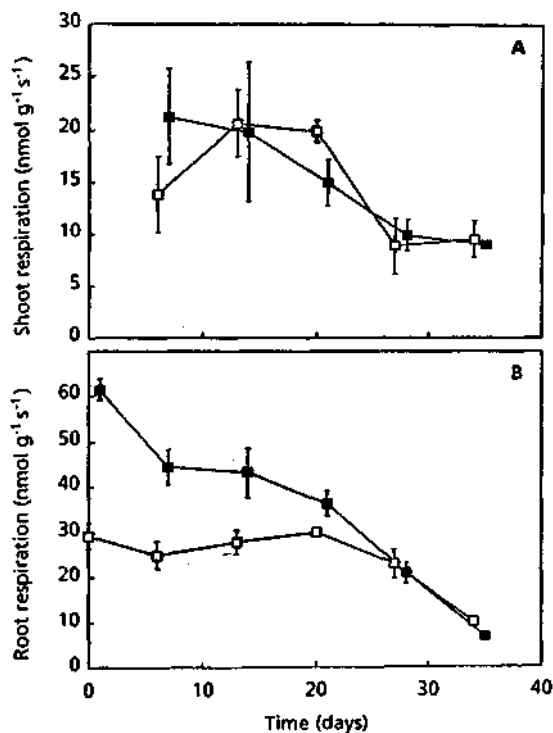

Fig. 2. Time course of the respiration of the shoot (*A*) and of the roots (*B*) of *Plantago major* ssp. *major* plants, grown at either 700 (■) or 350 (□) μmol mol^{-1} CO_2. Data are expressed per unit shoot weight and root weight respectively, and are derived from Poorter *et al.* (1988). Numbers on the *x*-axis refer to time after start of the CO_2 enrichment. Mean values $\pm$ s.e. ($n = 4$).

Carbon Content

A comparison in carbon content in high CO_2 and control plants is given in Table 2. On average there is a slight increase in the C-content of leaves *(P < 0.001)* and stem *(P < 0.001)*, whereas roots are not significantly affected. Moreover, both increases and decreases are found. How can this be explained? Carbon content is a reflection of the chemical composition of the plant (cf. Poorter 1989). Some of the chemical constituents have a high C-content (lipids, lignin, protein), whereas the C-concentration of others is low (organic acids) or nil (minerals). Insight into the alterations in C-content can therefore be obtained by analysing the (proximate) composition of the plant. For most groups of chemical constituents, little is known about changes caused by ambient CO_2 concentration. The only well-documented change is an increase in the concentration of starch and/or soluble sugars. Starch has a C-content of 0.0367 mol g^{-1}. Relative to starch, the total C-content of the dry mass of fast-growing species shows lower values, whereas slow-growing species show higher values (Poorter 1989; Poorter and Bergkotte 1992). Therefore, it could be expected that plant species with an inherently high C-content (> 0.0367 mol C g^{-1}) under normal ambient conditions should show a decrease in this element upon CO_2 enrichment, whereas species with a low C-content (< 0.0367 mol C g^{-1}) should show an increase due to the starch accumulation. We have tested this hypothesis, but did not find a negative correlation between carbon content at normal ambient CO_2, and the extent to which CO_2 enrichment increased the response ratio (Fig. 3). Therefore, on the basis of this rather limited amount of data we cannot support this hypothesis. Are there alternative explanations? Given that plants with an inherently high C-content also show an increase in response ratio, this implies changes in chemical composition apart from an increase in carbohydrates. Under high carbon availability sugars may replace minerals as osmotica, thereby decreasing mineral demand for vacuolar contents. Alternatively, compounds with a high carbon content and energy status (lignin, lipids) may accumulate to a greater extent. To our knowledge, these hypotheses have not yet been tested.

Table 2. Ratio of the carbon content of plants grown at high and at control levels of CO_2

Data are expressed per unit of organ dry weight. Average values per category are given after removing the 10% smallest and 10% largest observations in each category. *P* gives the probability that the ratio does not differ from 1. * *P < 0.05*; ** *P < 0.01*; *** *P < 0.001*

Species	CO_2		Ratio high: control			Reference
			Leaf	Stem	Root	
C_3 species						
Alnus glutinosa	350	700	1.01	1.02	1.02	H. Poorter, unpublished
Artemisia tridentata	350	650	0.96			Johnson and Lincoln 1990
Avena sativa	350	700	1.04	1.04	1.04	S.C. Wong, unpublished
Brassica pekinensis	350	700	1.03			S.C. Wong, unpublished
Eichhornia crassipes	350	700	1.01	1.02	0.99	Alpert *et al.* 1992
Elymus athericus	380	720	1.06	1.02		G. Lenssen and H, Poorter, unpublished
Eucalyptus camaldulensis	350	700	1.03	1.00	1.00	R.M. Gifford, unpublished
	350	700	1.00	0.99	0.98	S.C. Wong and P.E. Kriedemann, unpublished
Eucalyptus cypellocarpa	350	700	1.02	1.04	1.02	S.C. Wong and P.E. Kriedemann, unpublished
Eucalyptus pauciflora	350	700	1.03	1.02	1.05	S.C. Wong and P.E. Kriedemann, unpublished

Table 2 *(continued)*

Eucalyptus pulverulenta	350	700	1.00	1.02	1.00	S.C. Wong and
						P.E. Kriedemann, unpublished
Glycine max	350	700	0.99	1.00	0.99	R.M. Gifford, unpublished
Hordeum vulgare	350	700	1.03	1.07	0.98	S.C. Wong, unpublished
Lolium perenne	300	620	1.00			Overdieck and Reining 1986
Lycopersicon esculentum	300	1000	0.99			Ho 1976
	300	1000	1.02			Ho 1978
	350	700	1.02		1.01	B.R. Loveys, unpublished
Medicago sativa	350	700	1.00	0.95	1.02	R.M. Gifford, unpublished
Pinus radiata	350	700	1.02	1.00	0.97	R.M. Gifford, unpublished
Pisum sativum	350	700	1.07	1.04	1.03	R.M. Gifford, unpublished
	350	700	0.99	0.99	1.04	R.M. Gifford, unpublished
Plantago major	350	700	1.02	0.99	0.98	H. Poorter, unpublished
ssp. *major*						
Plantago major	350	700	1.02	1.01		Den Hertog *et al.* 1992
ssp. *pleiosperma*						
Scirpus olneyi	350	686	1.01			Curtis *et al.* 1989
Solanum tuberosum	350	700	1.04	1.08	1.03	P. Dijkstra and H. Poorter,
						unpublished
Triticum aestivum	350	700	1.05	1.06	0.90	R. Gifford, unpublished
	330	660	1.00			J. Masle, unpublished
	330	660	0.98			J. Masle, unpublished
	350	700	1.04	1.01		P. Dijkstra and H. Poorter,
						unpublished
Trifolium pratense	340	600	0.99	1.03		D. Overdieck and P. Ikels,
						unpublished
Trifolium repens	300	620	1.00	1.04		Overdieck and Reining 1986
Trifolium subterraneurn	350	700	1.00	1.03	1.01	R.M. Gifford, unpublished
Vitis vinifera	350	700	1.03	1.02	1.00	R.M. Gifford, unpublished
Mean value C$_3$			1.014	1.020	1.005	
P			***	***		
C$_4$ species						
Sorghum bicolor	350	700	0.95	0.98	1.06	R. Gifford, unpublished
Spartina anglica	380	720	1.00	1.01		G. Lenssen and H. Poorter,
						unpublished
Spartina patens	350	686	1.01			Curtis *et al.* 1989
Mean value C$_4$			0.989	0.992	1.057	
Mean Value C$_3$ and C$_4$			1.012	1.017	1.007	
P			***	***		

The Quantitative Importance of Changes in Respiration and Carbon Content

Respiration and carbon content appear not to be changed systematically by CO_2 enrichment, as both increases and decreases have been reported. Thus, in some cases these variables do not contribute to the growth stimulating effect at all. However, in other cases changes do occur. Are these changes important enough to contribute to a growth stimulating

effect or, alternatively, mask the effect of the increased photosynthate supply? To obtain insight into this question we carried out a sensitivity analysis. To this end we started with a hypothetical plant with an intermediate relative growth rate of 0.2 g g^{-1} day^{-1}. The relevant values for each of the terms of equation (1) were taken from an experiment with 24 wild species (Poorter and Remkes 1990; Poorter *et al.* 1990). These values are listed in Table 3. From Poorter (1992) we inferred an average stimulation of 41% in dry mass due to CO_2 treatment acting on a C_3 plant, and we assumed this would happen in 20 days. For both respiration and carbon content we calculated within what range shifts are most likely to be found. The distribution of a parameter can be characterised by percentile values, which indicate the value below which a given percentage of the observations is found. In addition to the average (or 50th percentile), we calculated the 20th and 80th percentiles of the ln-transformed ratios. Given these percentiles and the averaged values of the response ratios, we then determined for leaf + stem and root respiration on one hand, and the carbon content of the three organs on the other, what change in RGR would be expected. We started from the situation where the 41% growth stimulation is thought to be due to changes in the carbon gain only, and we calculated how large the growth stimulation would be, if we introduced the observed changes in respiration and C-content in equation (1). This enabled us to calculate what the growth stimulating effect would be, if we were to take these changes into account.
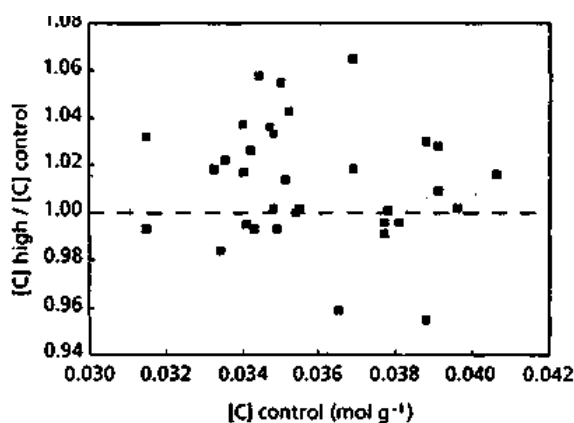

Fig. 3. Ratio of the leaf carbon content, expressed per unit leaf dry weight, of high CO_2 and control plants, plotted against the leaf carbon content of the control plants. Data are those from Table 2, except for values of Ho (1978), which showed much lower C-content than the others (but similar response ratio) and were excluded from this analysis.

The mean values and the 20th and 80th percentiles in the response ratio of respiration rates and C-content are listed in Table 4. The last column shows percentage change in the growth stimulating effect that would occur for a given increase in respiration rate or C-content of all organs. If, for example, inclusion of secondary changes produced a 82% rather than a 41% stimulation in weight, then the percentage change would be 100.

As can be seen in Table 4, the average change in respiration rate increases growth by only 3%. The decrease in growth due to the average increase in C-content is also small (15%). However, if we consider the 20th and 80th percentiles in these parameters, the situation is different. In a number of cases, changes in respiration are so important that they almost equal the observed stimulation in the average experiment. In other words: the change in dry weight due to the effect of high CO_2 on respiration might be of similar magnitude to the average change in yield reported in the literature. The implication of this result is that a large part of the variation in yield response, as observed in the different published experiments (cf. Poorter 1992), might be due to variation in respiratory adjustments under elevated CO_2. Similarly, the change in C-content might also contribute to this variation, albeit to a lesser extent.

Table 3. Values of the variables of equation (1),
as used in the sensitivity analysis

Parameter	Value
PS_a	$448.9*10^{-3}$ mol C m^{-2} day^{-1}
LR	$2894*10^{-6}$ mol C g^{-1} day^{-1}
SR	$2894*10^{-6}$ mol C g^{-1} day^{-1}
RR	$4847*10^{-6}$ mol C g^{-1} day^{-1}
SLA	$38.6*10^{-3}$ m^{2}g^{-1}
LWR	0.53 g g^{-1}
SWR	0.18 g g^{-1}
RWR	0.29 g g^{-1}
LCC	$35.7*10^{-3}$ mol C g^{-1}
SCC	$34.1*10^{-3}$ mol C g^{-1}
RCC	$33.0*10^{-3}$ mol C g^{-1}

Table 4. The observed response ratio of the carbon content of leaves (LCC), stem (SCC) and roots (RCC), and of leaf plus stem respiration (LR, SR) and root respiration (RR) upon CO$_2$ enrichment

Average values (50th) as well as the 20th and 80th percentiles are given. The last column (% response) indicates the extent of increase in dry weight, given a certain increase for independent variables, and normalised for the average growth response of a C$_3$ herb to a doubling in the atmospheric CO$_2$ concentration (41%). For further information see text

Percentile	LCC	SCC	RCC	LR,SR	RR	% response
20th	0.995	0.998	0.984			11
50th	1.012	1.017	1.007			-15
80th	1.032	1.036	1.031			-41
20th				0.767	0.923	67
50th				1.030	0.972	3
80th				1.348	0.994	-53

Four assumptions underlie these calculations.

First, that plant growth is in steady state, i.e. relative growth rates, carbon exchange rates, allocation and C-content were stable within a treatment during the 20 day growth period.

Second, we assumed that stem respiration per unit stem weight was equal to the carbon gain of the same organ during the day, and to be equal to the rate of leaf respiration per unit leaf weight during the night.

Third, we conceptualised that the parameters of equation (1) are independent of each other.

Fourth, it should be noted that in Table 1 many more data are available for the rate of leaf respiration expressed per unit area than expressed per unit weight. In order to include this additional information, we converted those values to a weight basis, assuming a similar

decrease in SLA as in those cases where data were expressed both ways (ratio on a weight basis = 0.892 * ratio on an area basis).

This sensitivity analysis is rather independent of the set of parameters chosen. Results are essentially similar when a plant with an RGR of 0.3 g g^{-1} day^{-1} and a stimulation in weight of 50% is chosen. The assumption of a steady state in growth, physiology and carbon allocation might be more critical. Therefore, a more thorough analysis of time patterns in growth and carbon economy in response to CO_2 enrichment is needed. However, even excluding the 40% most outlying observations, the effects of variation in both C-content and respiration in the above-mentioned analysis are so large that respiration and chemical composition may contribute considerably to the observed variation in the growth response of plants to high CO_2.

Conclusions

The effect of high CO_2 concentrations on respiration rates and C-content is variable. At present there is insufficient insight into the causes of this variability. On average, the CO_2 induced changes in respiration and C-content are small, but variability is such that in some cases changes may affect the growth stimulation to a major extent. Therefore, these variables should be included in any analysis of mechanisms by which CO_2 stimulates growth.

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