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Plant Growth at Elevated CO$_2$

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Elevated carbon dioxide (CO$_2$) concentrations stimulate the rate of photosynthesis of most plant species. Consequently, it is expected that prolonged growth of plants at increased atmospheric CO$_2$ concentrations will enhance their biomass. This prediction is in agreement with most experimental results performed at optimal growth conditions. However, plant growth is stimulated less than expected on the basis of the increased rate of photosynthesis per unit leaf area. This is due to the fact that plants at elevated CO$_2$ have reduced leaf area on display per unit biomass, thereby decreasing the relative amount of machinery. The reduction goes with increased accumulation of non-structural carbohydrates.

The magnitude of the growth response to elevated CO$_2$ depends on the plant species. Species like maize and millet, which have a special type of photosynthesis, show a marginal growth response to elevated CO$_2$ (on average 11%). However, most plant species respond more strongly, with an average stimulation in biomass of 47% for a doubling of the present atmospheric CO$_2$ level. Inherently slow-growing species are generally less responsive than fast-growing species. The growth response also depends on the level of other environmental factors. In nutrient-poor and cold environments the proportional growth stimulation by elevated CO$_2$ will be less. There is a slight increase in response when levels of light and water are decreased. The strongest interaction is with ozone, with plants showing a much stronger CO$_2$ response when ozone concentrations are higher.

Elevated atmospheric carbon dioxide (CO$_2$) concentrations generally have two direct and momentary physiological effects on plants. First, they increase the rate of photosynthesis of the leaves, because of higher CO$_2$ concentrations at the sites where enzymes fix CO$_2$. Second, they cause stomata to partly close, thereby reducing the water loss due to transpiration. Thereafter, secondary effects may occur, when plants experience elevated CO$_2$ concentrations for a longer time. Respiration rates may decrease or increase, chemical composition of the plant may change, and so may leaf morphology and anatomy. For a review of the effect of CO$_2$ on these physiological processes (*see* **Plants – Carbon Balance and Growth**,

Volume 2). In this contribution, we analyze how the myriad of direct and indirect changes affects the growth of individual plants in the vegetative stage. First, plant growth responses under relatively optimal conditions will be discussed. Thereafter, we will consider CO$_2$ effects under conditions limiting for plant growth. Responses are analyzed by compiling literature data for a large range of published experiments on individually growing whole plants, grown either in growth chambers, glasshouses or open-top chambers.

GROWTH STIMULATION DOES NOT ONLY DEPEND ON THE STIMULATION OF PHOTOSYNTHESIS

The growth of a plant over time can be adequately described by the relative growth rate (RGR; see Box 1 for more information). Mathematically, this variable is the product of three biologically meaningful growth parameters: ULR, SLA and LMF. The ULR is the biomass increase per unit leaf area and time, and is a composite parameter that includes the daily rate of photosynthesis per unit leaf area, the fraction of fixed carbon that is respired the same day and the carbon content of the plant material. SLA is the amount of leaf area formed per unit leaf biomass, a parameter linked to the light-intercepting capacity of a leaf. The LMF is the relative amount of total plant biomass invested in leaves, and thus in the process of carbon fixation.

How are RGR and its components affected by elevated CO$_2$? We analyzed 130 observations on the growth of species with the most common type of photosynthesis (C$_3$ species) from 50 published experiments (see Poorter and Nagel, 2000). For each growth parameter we calculated the ratio between the value at elevated CO$_2$ (approximately 70 Pa) and that at current levels (approximately 35 Pa). The distribution of these ratios is shown in Figure 1. On average, the RGR is stimulated to a small extent (9%). The increase can be attributed to an increase in ULR (23% on average). Although both respiration and carbon concentration may change to some extent (Bunce, 1994; Poorter *et al.*, 1997), it is mainly the stimulation in the rate of photosynthesis per unit leaf area that increases ULR. At the same time, the SLA decreases (13% on average), which implies that plants grown at elevated CO$_2$ have less leaf area on display per gram of leaf. This decrease in SLA counteracts the increased rate of photosynthesis per unit leaf area, the net result being that growth is stimulated substantially less than was expected on the basis of the stimulation in the rate of photosynthesis alone. The decrease is at least partly linked to the accumulation of starch and other non-structural carbohydrates (Körner *et al.*, 1995). The most likely reason for the accumulation is that plants have increased photosynthesis to the

Box 1	Terminology used. All biomass data presented in this article are on a dry weight basis		
Abbreviation	Full term	Definition	Units
BER	Biomass enhancement ratio	Biomass at elevated CO_2/biomass at control levels	$g\,g^{-1}$
LMF	Leaf mass fraction	Fraction of biomass allocated to leaves	$g\,g^{-1}$
RGR	Relative growth rate	Increase in biomass per unit biomass already present and per unit time	$m\,g\,g^{-1}\,day^{-1}$
SLA	Specific leaf area	Leaf area per unit leaf biomass	$m^2\,kg^{-1}$
ULR	Unit leaf rate	Increase in biomass per unit leaf area and time	$g\,m^{-2}\,day^{-1}$
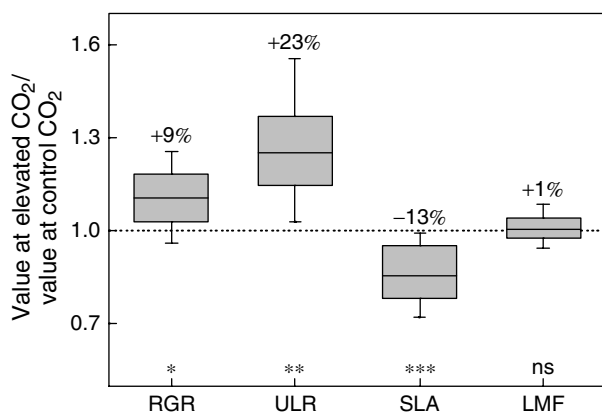
Figure 1 Effect of elevated CO_2 on RGR and its components ULR (g dry mass increase m^{-2} leaf area and day^{-1}), SLA (m^2 leaf area per kilogram leaf mass) and LMF (g leaf per gram total plant). The effect is calculated by dividing the value at elevated CO_2 by the value at ambient levels of CO_2. Results from 130 growth analyses (compiled in Poorter and Nagel, 2000) are shown as boxplots. The numbers above the boxplots are the average percentage increases due to elevated CO_2 (10%-trimmed means). Boxplots indicate the distribution of a range of observations. The lower part of the box shows the 25th percentile, the value below which 25% of the observations are found. The highest part of the box gives the 75th percentile, and the line in between the median (50th percentile). The error bars give the 10th (lower) and 90th (higher) percentile. Significance levels for the H_0-hypothesis that the ratio equals 1 are indicated above the *x*-axis: ns, non-significant; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

extent that they cannot usefully deploy the newly fixed carbohydrates into new growth. They are then accumulated as non-structural carbohydrates in the leaves, causing the SLA to decrease. The last parameter involved, the LMF, hardly changes (1% increase on average), indicating that biomass allocation is generally not affected by elevated CO_2 (Stulen and Den Hertog, 1993). In the end, it is the net balance of all these physiological and morphological changes that determines the overall growth response of plants to elevated CO_2, and not only the response of leaf photosynthesis.

GROWTH STIMULATION IS TIME-DEPENDENT

Given the possible feedbacks discussed above (changes in physiological processes, biomass partitioning between plant parts and chemical composition), it is difficult to forecast the growth response of plants from short-term effects on the rate of photosynthesis and transpiration alone. This problem becomes even larger as the growth stimulation turns out to be time-dependent. In quite a number of studies, RGR is increased by elevated CO_2 only at the beginning of the experiment, the growth stimulation lasting *circa* 5–15 days. Thereafter, growth rate becomes more or less equal to that of plants at ambient CO_2. In the rest of this contribution, we will use the ratio of plant biomass at elevated and at ambient levels of CO_2 as a measure of the growth response of plants. We will call this the BER (*biomass enhancement ratio*). If RGR were only stimulated during the first 10 days of CO_2 enrichment, BER would start at a value of 1 at the beginning of the experiment, increase up to a certain level until day 10, and then remain constant (Figure 2a, broken line). Particularly in longer-term experiments with tree seedlings, it has been reported that BER even decreases after the first year of the experiment (Figure 2b). In this contribution we will not discuss possible differences in duration between experiments, the reader is referred to reviews like Poorter (1993) and Curtis and Wang (1998).

GROWTH STIMULATION DIFFERS BETWEEN GROUPS OF SPECIES

While keeping in mind that the growth stimulation may be time-dependent, it would be useful to condense the information from the numerous experiments on elevated CO_2 that have been carried out with a wide range of plant species. We did so by screening the literature, restricting our analysis to experiments where plants were grown at elevated CO_2 levels between 60 and 80 Pa, and at control levels of CO_2 between 30 and 40 Pa. For each experiment and each species where whole plant dry mass was

(a)

Duration of CO$_2$ enrichment
(days)

(b)

Duration of CO$_2$ enrichment
(years)
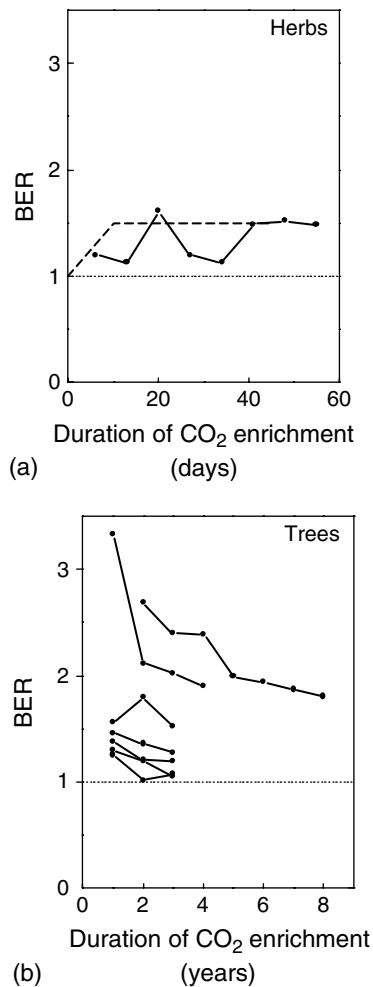
Figure 2 Time course of the BER due to elevated CO$_2$. (a) An example of an idealized response (bold line) and the response of a herbaceous species. (b) The observation for some tree species

determined, we calculated the BER, arriving at a total of 600 observations (for more information see Poorter, 2001). These were first averaged per species, and subsequently species were classified into a limited number of groups that we thought to have important characteristics in common. Such a separation into functional types may increase insight into the differential response of groups of species and enables generalization of the results. The first distinction we made was on the basis of the type of photosynthesis. Most species fix CO$_2$ during the day, and experience relatively low levels of CO$_2$ at the actual site of fixation (so-called *C$_3$ plants*) (*see* **C$_3$ and C$_4$ Photosynthesis**, Volume 2). A number of species, like maize and millet, have a very efficient way to increase the CO$_2$ concentrations to high levels at the place in the leaf where carbon is fixed (so-called *C$_4$ plants*), even at low ambient concentrations of CO$_2$. Purely on that basis they can be expected to respond less to an

increase of CO$_2$ in the atmosphere than C$_3$ species. Other species, like cacti, take up CO$_2$ from the air during the night but actually incorporate that carbon into carbohydrates during the day (crassulacean acid metabolism (*CAM*) species). The C$_3$ species respond most strongly to elevated CO$_2$, with an average increase in biomass of 47% (Figure 3). Data on CAM species are scarce; the mean response for the 6 species investigated being 21%. Rather unexpectedly, C$_4$ species also respond to increased CO$_2$ levels (11%). This might be due to increased rates of carbon fixation at elevated CO$_2$ in some C$_4$ species. Another explanation might be that in some experiments plants were thought to grow under optimal conditions, when in fact they were suffering from water stress to some extent. Then, the partial closure of the stomata caused by elevated CO$_2$ was advantageous for their water balance and would have enhanced growth by alleviating stress (see next section). Such an effect may play a role in experiments with C$_3$ species as well.

The second distinction we made was within the group of C$_3$ species. On average, crop species show the highest biomass enhancement (59%) and wild herbaceous plants the lowest (41%). Most of the experiments with woody species have been carried out with seedlings, thus covering only a small part of the life cycle of these plants. Their growth stimulation is on average 49%. Crop species are generally fast growing. The herbaceous wild plants consist of a wide mix of species, some growing as fast as crop species, others almost as slow as tree seedlings. It has been suggested that inherent variation in RGR may account for part of the interspecific variation between C$_3$ species (Poorter, 1993). Indeed, inherently slow-growing species respond
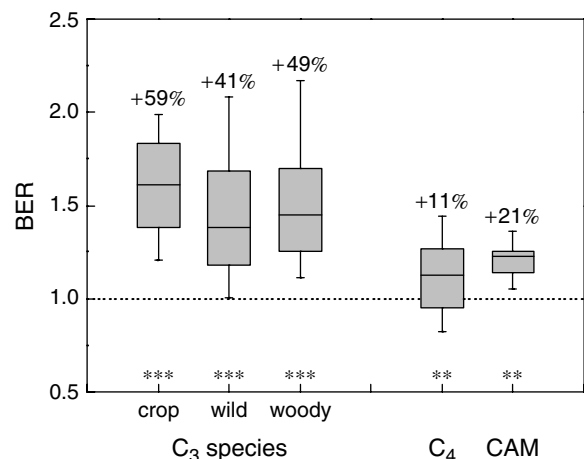

Figure 3 Distribution of BER for several functional types of species. Distributions are based on 540 observations from 280 C$_3$ species; 55 observations from 30 C$_4$ species; 13 observation from six CAM species. C$_3$ species were separated into three groups. There were 110 observations from 24 crop species; 190 from 115 wild herbaceous species; and 230 from 135 woody species. (Literature data compiled in Poorter, 2001)

generally less (27% on average) than the category of fast-growing species (60% on average). This generalization is confirmed in most experiments where fast- and slow-growing species are compared for their BER. Two examples for herbaceous species and two for woody species are shown in Figure 4. Although the correlation is not always statistically significant, in all research on the response of a range of species, the slope of the line that fits the BER versus RGR data is found to be positive (Poorter, 2001). Most likely, it is the balance between the carbohydrates supplied by photosynthesis and those utilized in structural growth and/or specialized storage organs that determines the degree of response to elevated CO_2. This may explain why fast-growing species, or species with storage sinks as tubers are among the species showing the stronger responses (Reekie *et al.*, 1998).

GROWTH STIMULATION DEPENDS ON THE LEVEL OF PRIMARY RESOURCES

The former analysis was for plants that were grown under laboratory conditions at levels of nutrients, light and water that are generally optimal or close to optimal for growth. What will happen if one of the primary resources is in short supply and causes a growth limitation? Given that both control as well as CO_2 enriched plants would be hampered in growth, one may expect that the absolute growth stimulation by elevated CO_2 will decrease. This is indeed the case. But what will happen to the relative growth stimulation? We compiled experiments that have been carried out at ambient and elevated levels of CO_2, and with high and low levels of the three primary resources (nutrients, light and water) (Poorter and Pérez-Soba, 2001). The severity of the stress was expressed by calculating how
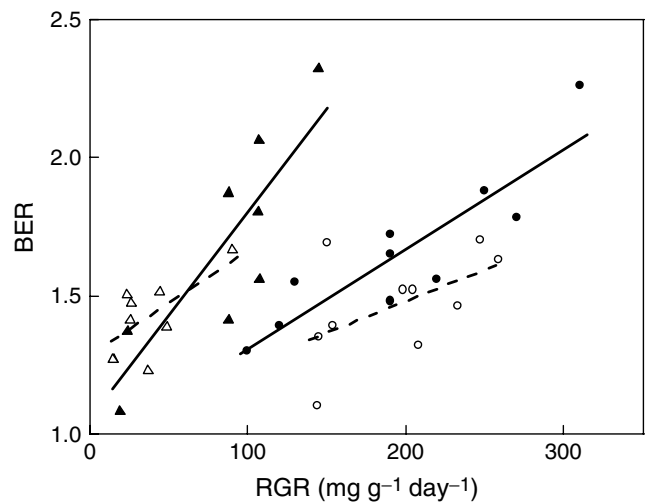
Figure 4 BERs of different species as a function of their RGR at ambient CO_2. All data pertain to C_3 species. Open triangles: temperate woody seedlings (Cornelissen *et al.*, 1999); closed triangles: tropical woody seedlings (Winter and Lovelock, 1999); closed circles: herbaceous crop and weed species (Bunce, 1997); open triangles: herbaceous wild species (Poorter, 1993). Continuous lines are regression lines that differ significantly from zero ($P < 0.05$), broken lines are non-significantly different

much the biomass of sub-optimally grown plants at ambient levels of CO_2 was reduced relative to the biomass of the optimally grown plants at the same CO_2 level. We then calculated the BER at sub-optimal and optimal conditions, and subsequently the slope of the line that connects the two BER values. If the slope is positive, it implies that BER increases when a primary resource becomes growth limiting. An example is given in Box 2.

Box 2 Calculating the effect of limiting factors on the BER

To analyze how elevated CO_2 interacts with another environmental factor at the level of plant growth, a minimum of four observations is required: the mass of plants at ambient and elevated CO_2 levels at both a low and high level of the other environmental factor. In Figure 5, an example is given for the interaction with ozone. Assuming that the mass of plants is as given in the insert, then the BERs are 1.5 and 2 at low and high ozone concentrations, respectively. It is difficult to assess the severity of the ozone stress just from a description of the experimental design. Therefore, as a measure of the stress experienced by the plants, we use the growth reduction shown by the high-ozone plants at ambient CO_2, scaled relatively to the mass of the high-ozone plants at ambient CO_2. If that fraction is close to 0, the stress was minor; if the fraction is much higher, then the ozone stress was apparently more severe. The BER value of the low-ozone plants is plotted at $x = 0$. The BER value of the high ozone plants is plotted at $x = 0.6$, this value being the growth reduction due to the high ozone

concentration. After plotting these ratios, the slope of the line connecting the points is calculated. A positive slope indicates that at high ozone concentrations, the relative increase of plant biomass by elevated CO_2 is larger. Note that in absolute terms, high-ozone plants at elevated CO_2 are still smaller than low-ozone plants at elevated CO_2.

The advantage of this approach is that the same procedure can be followed for other environmental variables, just replacing the low ozone treatment with, for example, low water supply or high SO_2. In the case of temperature there is an optimum rather than a linear response. Here we selected the treatment with the highest biomass as the optimal one. A disadvantage of the approach followed is that the analysis implicitly assumes that the BER changes linearly across the range of another environmental factor from sub-optimal to optimal. For the calculations, all BER values have to be transformed prior to any mathematical analysis, as ratios are log-normally distributed. The slope in this case is 0.48.
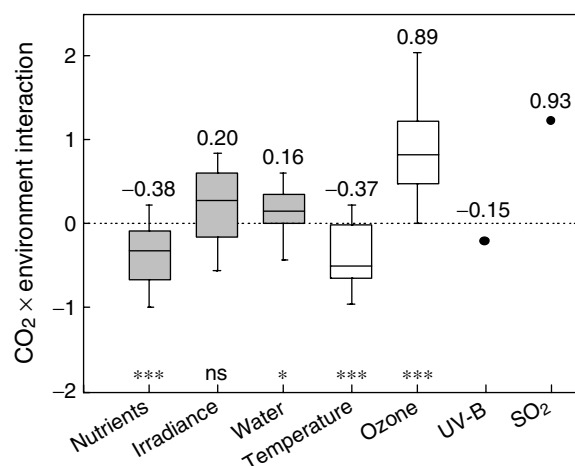
The distribution of the slopes for a range of experiments is represented by the boxplots of Figure 6. On average, the slope is negative in the case of nutrients. This implies that a decrease in nutrient availability decreases the relative response of plants to elevated CO$_2$. The pattern of responses was similar between experiments where nitrogen, phosphorus, or all nutrients together were varied. It seems that at ambient CO$_2$ conditions the growth of plants at low nutrient levels is not restricted by carbon availability, since high concentrations of starch and other non-structural carbohydrates are found in nutrient-stressed plants. Consequently, an increase in the carbohydrate pool due to an increase in photosynthesis by elevated CO$_2$ concentrations is not expected to stimulate growth to a large extent.

The slope is positive for the factor irradiance, but variability is high and the mean does not differ significantly from zero. A positive slope would imply that at low irradiance the response to elevated CO$_2$ is relatively stronger than at higher irradiance. It has been suggested that elevated CO$_2$ decreases the light compensation point of photosynthesis (*see* **Plants – Carbon Balance and Growth**, Volume 2). However, that would only hold at very low irradiance levels (Kimball, 1986a). Elevated CO$_2$ causes a partial closure of stomata, which in turn reduces plant water use. Therefore, plants growing at limited water availability might thrive longer on a given water supply. The relative growth response is expected to be higher, and this is indeed what has been observed (Figure 6). However, on average the interaction with water is small.

It should be noted that, in general, interactions can be expected between these primary resources: at low water supply, nutrients will be less mobile, and at high irradiance, plants will grow faster, with a higher chance of nutrient or water depletion around the roots.
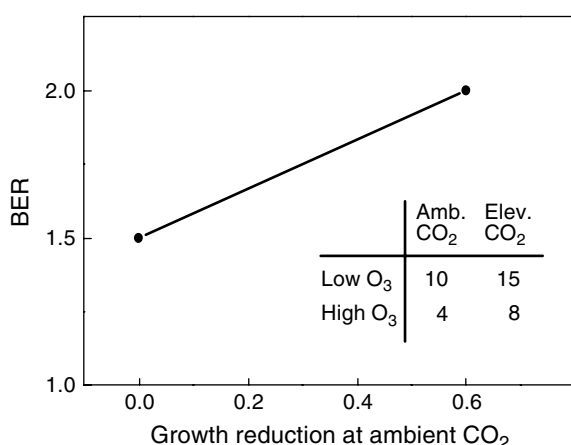
Figure 6 Interaction between elevated CO$_2$ and various environmental factors on plant growth. Boxplots give the distribution of the slopes, obtained as outlined in Box 2. Values below zero indicate that the relative stimulation of plant growth by elevated CO$_2$ is smaller at growth-limiting levels of the various factors under investigation. Values above zero indicate that the BER is larger. Data are based on a literature review (Poorter and Pérez-Soba, 2001) on factorial experiments with combinations of elevated CO$_2$ and nutrients ($n = 102$ observations), irradiance ($n = 19$), water ($n = 29$), temperature ($n = 56$), O$_3$ ($n = 24$), UV-B ($n = 7$) or SO$_2$ ($n = 3$). Due to the low number of observations for UV-B and SO$_2$ we only calculated the average values. Significance levels are given for the v-hypothesis that the slope equals zero

CO$_2$ INTERACTS WITH OTHER GLOBAL CHANGE FACTORS

Global change is not restricted to an increase in the atmospheric CO$_2$ concentration. Increases in temperature due to the accumulation of greenhouse gases such as CO$_2$, methane and chlorofluorocarbons are anticipated as well. Moreover, because of anthropogenic activities, atmospheric ground-level concentrations of ozone (O$_3$), nitrogen oxide (NO$_x$) and sulfur dioxide (SO$_2$) are rising, and so is the UV-B radiation. How will these factors influence plant growth responses to rising atmospheric CO$_2$ concentrations? We followed the same approach as in the previous section, analyzing factorial experiments in which both CO$_2$ and one of these other environmental factors were investigated. Once more, we calculated the growth reduction under suboptimal conditions relative to the optimal one and determined the slope of the line connecting the two BER values.

The interaction of CO$_2$ with supraoptimal temperatures has hardly been investigated. On average there is a smaller growth response to elevated CO$_2$ at temperatures suboptimal for growth (Figure 6; cf. Idso and Idso, 1994). One explanation is that elevated CO$_2$ stimulates photosynthesis relatively less at lower temperatures. Another is

Figure 5 The CO$_2$ response of plants that grow under a low concentration of ozone (at $x = 0$) or at a high concentration. The insert gives the hypothetical biomass data on which the graph is based

that at suboptimal temperatures, growth is inhibited more than photosynthesis, causing non-structural carbohydrates to accumulate. As with low nutrient availability, this may preclude a strong response to increased CO_2. For those plant species that currently grow under sub-optimal temperatures, one may expect a greater CO_2 response if a global warming of the climate takes place.

Ozone shows the strongest positive interactions with CO_2 (Figure 6). For almost all observations, the slope is positive, implying that CO_2 strongly ameliorates the effect of ozone. There is good evidence that in plants in which stomatal conductance is reduced by CO_2 enrichment, O_3 flux into the leaf interior is reduced and this contributes to an amelioration of the detrimental effects of O_3 on plant growth and physiology (Turcsányi *et al.*, 2000). It is yet not clear to what extent other mechanisms induced by elevated CO_2 may play a role in amelioration, such as detoxification or repair processes. A second point of concern is the strength of the combined effect of elevated CO_2 and O_3 on the growth and productivity of species in which the stomata are less responsive to CO_2 enrichment, such as many conifers. Data indicate that for those species, there may be similar effects of O_3 at ambient and elevated CO_2, or at least much less amelioration of ozone damage than that observed in herbaceous species (Pérez-Soba *et al.*, 1995).

Experiments with $CO_2 \times UV-B$ interactions are scarce, the data hinting at the fact that elevated CO_2 could not compensate for the harmful effect of UV-B (Figure 6). However, these results obtained under artificial environmental conditions could result in responses different from the field situation. First, the UV-B levels used in the experiments are generally very high. Second, leaves developed under full sunlight have morphological and physiological adaptations that afford some protection from UV-B (Teramura and Murali, 1987). Consequently, plants in growth chambers, in which the visible light levels (*photosynthetically active radiation*) (*see* **PAR (Photosynthetically Active Radiation)**, Volume 2) are about two times lower than in field conditions may be more sensitive to UV-B than those in the field. The information on combined effects of elevated CO_2 and SO_2 or nitrogen (N) deposition is so limited that it precludes any generalized statement.

To summarize the effects of elevated CO_2 at sub-optimal growth conditions, we plotted the average BER values against the average growth reduction observed in the compiled literature (Figure 7). The growth enhancement by elevated CO_2 is severely reduced at low temperatures or poor nutrient supply. On the contrary, it is increased at low soil water availability, but the rise in BER is only small. The interaction between elevated CO_2 and O_3 shows the most dramatic response. The loss of biomass due to elevated ozone is, on average, more than compensated in the presence of elevated CO_2.
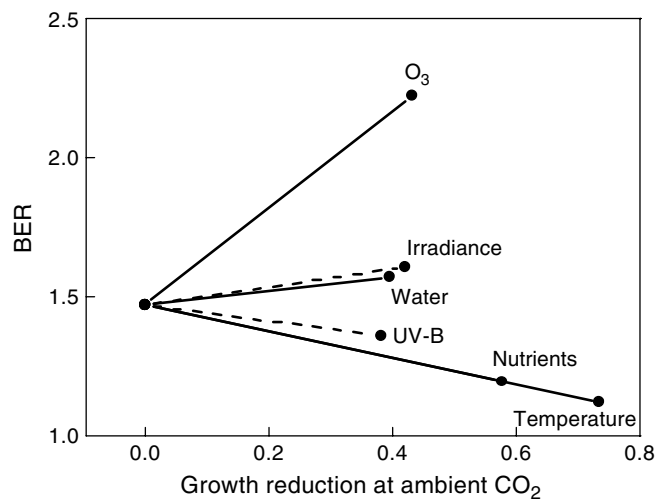
Figure 7 The average growth response of plants when elevated CO_2 is combined with sub-optimal levels of other environmental factors. Responses were calculated using a BER of 1.47 for plants grown under optimal conditions (Poorter, 1993). The average slope was calculated from the data of Figure 6 and the average reduction in growth at 35 Pa CO_2 as calculated in the compiled literature

AN OUTLOOK

Up to now we have focused on experiments that have been carried out with individual plants in the vegetative stage. When extrapolating these results to the field situation, the following considerations should be taken into account. First, we have focused on average responses based on underlying data that are quite variable, partly due to the different growth conditions between experiments. Second, part of the increase in biomass is due to the accumulation of high levels of non-structural carbohydrates. This part of the extra-achieved biomass does not necessarily add to the performance of the plant and therefore may be regarded as non-functional in a number of cases. Third, generative biomass (seeds, fruits) is often stimulated to a lesser extent than vegetative biomass, at least in crop species (26% on average, Kimball, 1986b). In addition, it is not necessarily true that the species stimulated strongly in the vegetative phase will also be those that are stimulated relatively stronger in generative biomass (Ackerly and Bazzaz, 1995). Fourth, plants growing in monoculture have been shown to respond less than individually grown plants (Wayne and Bazzaz, 1995). Finally, most research was carried out with plants that have not been able to adapt genetically to high CO_2 levels.

How do growth responses of laboratory-grown individual plants, grown at optimal conditions, compare to those in the field? The above-ground biomass of monocultures of plants grown under agricultural field conditions increases by 20–40% due to elevated CO_2. This increase is somewhat smaller than that found in Figure 3. On the basis

of the strong interaction with nutrients (Figure 7), it can be expected that natural types of vegetation, where plants are generally growing under far less fertile conditions, will show even smaller responses in biomass production. Current information shows that this is indeed the case, above-ground biomass in CO_2 enriched grasslands being increased by 14% on average (Mooney *et al.*, 1999). A discussion on the effects of elevated CO_2 on ecosystem functioning is given by Körner (*see* **CO_2 Enrichment: Effects on Ecosystems**, Volume 2).

ACKNOWLEDGMENTS

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